Ecological enhancement of an aphid parasitoid

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CONTENTS

ABSTRACT

Insects have become increasingly resistant to chemical control methods, while at the same time public awareness of the harmful effects of synthetic pesticides has increased. The search for more environmentally 'friendly' means of pest suppression is gaining momentum and biological control (the use of natural enemies to reduce populations of noxious organisms) has become an increasingly sought-after option.

Despite an increase in the establishment rate of insect natural enemies, classical biological control of arthropods is currently no more successful than it was one hundred years ago. Ecological theory relevant to population biology, food webs and diversity provides insight into how biological control agents can be made more effective, yet this theory has often been absent from the biological control literature. Examples of the use of ecological concepts (including intraguild predation, life-history omnivory and resource subsidies) in practical biological control are reviewed, and aspects of theory not yet considered in this context are discussed.

Cereals are important as primary food crops, globally and within New Zealand. Possibly the greatest amount of damage sustained by cereal crops in New Zealand is caused by aphids and chemical control of these pests is very expensive relative to biological control. This thesis examines how biological control of the rose-grain aphid *Metopolophium dirhodum* (Walker) (Hemiptera: Aphidiidae) by the koinobiont, synovigenic endoparasitoid *Aphidius rhopalosiphi* De Stefani-Perez (Hymenoptera: Aphidiidae) can be enhanced by floral resource subsidies. The mechanisms underlying this enhancement were determined in a series of laboratory experiments and then tested in laboratory microcosms and in the field.

Sugar resources significantly increased longevity and egg load in *A. rhopalosiphi* and another species of aphidiid, *Diaeretiella rapae* McIntosh. Pollen had no significant effect on longevity or egg load in these species. These results are discussed in terms of the effects of resource subsidies on egg- versus time-limitation.

Laboratory microcosm experiments tested whether the mechanisms of increased potential fecundity via enhanced egg load and longevity translate into increased rates of

parasitism (i.e., realised fecundity). Only treatments receiving sugar showed increased reproductive success. The presence of flowering buckwheat *Fagopyrum esculentum* Moench (c.v. Kitawase) (Polygonaceae) plants caused a slight, non-significant increase in rates of parasitism.

Field surveys of natural aphid populations in a wheat *Triticum aestivum* (L.) (c.v. Otane) (Gramineae) field showed that proximity to floral buckwheat patches, distance to the nearest edge or the leeward end of the field were not significantly correlated with rates of parasitism. These variables were significantly correlated with aphid density in some surveys. Rates of parasitism were not correlated with aphid density. When aphid population density was controlled by experimental placement of aphids, proximity to floral resource patches significantly affected rates of parasitism. Parasitism rates were highest at the edges of buckwheat patches and declined exponentially with distance, eventually reaching zero beyond 14 m. Lower levels of parasitism were observed within the floral patches than at their edges. This phenomenon is compatible with the concept of spatio-temporal partitioning between parasitoid feeding and host-searching behaviours.

Potential costs (increased predation risk, opportunity costs) and benefits (increased fecundity and longevity) associated with floral feeding by parasitoids, and temporal variation in these factors, are discussed. It is concluded that resource subsidies are not only effective in the practical enhancement of the efficacy of a specific biological control agent, but their use is based on a sound foundation in ecological theory that allows extension of these principles across taxa.

CHAPTER 1: INTRODUCTION

WHY USE BIOLOGICAL CONTROL?

As public awareness of the harmful effects of synthetic pesticides (e.g., Paoletti & Pimentel 2000) has increased, the search for more environmentally 'friendly' means of pest suppression has gained momentum (e.g., DeBach & Rosen 1991; Hokkanen *et al*. 1995; van Driesche and Bellows 1996; Pimentel 1997). At the same time, insects have become increasingly resistant to chemical control methods, to the extent that pesticides are less effective now than in the past, even at increased dosages (Georghiou & Taylor 1977; Eichers 1981; Price 1991; Sun & Sun 1994; Palumbi 2001).

Biological control can be defined as the use of natural enemies to regulate noxious organisms (adapted from definitions by DeBach & Rosen 1991). It has become an increasingly sought after option (e.g., United States Congress Office of Technology Assessment 1995), as it is potentially long-lasting (DeBach & Rosen 1991), relatively inexpensive (DeBach & Rosen 1991; Greathead 1995) and, when implemented correctly, less harmful to the environment than other methods of pest control (DeBach & Rosen 1991; Carruthers & Onsager 1993; Perkins & Patterson 1997; but see Howarth 1991; Greathead 1995; Simberloff & Stiling 1996; Gurr & Wratten 2000b; Howarth 2000; Hopper 2001).

Biological control is, by definition, an ecological phenomenon, in which trophic interactions or even entire food webs are manipulated for human benefit. It is this ecological basis that makes the study of biological control theoretically, as well as financially rewarding. However, the complexity inherent in any ecological system requires detailed understanding through theoretical and empirical analyses before interactions can be manipulated in a predictive manner. It is not enough merely to observe direct, 'beneficial' species interactions and attempt to recreate them in an agricultural setting. The mechanisms driving these interactions, and their indirect effects on other organisms, must be fully understood before a biological control programme can be considered to be truly effective and environmentally responsible (Waage 1990; Ehler 1994; Sheehan 1994; Kareiva 1996; Simberloff & Stiling 1996, Berryman 1999, Gurr & Wratten 1999, Landis *et al.* 2000; Hopper 2001; Strong & Pemberton 2001).

SPECIES AND METHODS USED IN BIOLOGICAL CONTROL

The natural enemies used for biological control are as numerous and varied as the organisms to which they are targeted. This thesis focuses on parasitoids (insect parasites that kill their host to complete their life cycle); however, predators, fungi, nematodes, bacteria and viruses are all used in biological control (for recent reviews of biological control using these organisms see van Driesche and Bellows 1996; Federici 1999; Hagen *et al.* 1999; Flexner & Belnavis 2000; Gordh *et al.* 1999; Orr & Suh 2000).

Natural enemies are employed using three major methods; i) importation of exotic species; ii) augmentation of existing natural enemy populations through direct propagation and release of individuals (generally referred to simply as 'augmentation'); and iii) augmentation of existing natural enemy populations through indirect enhancement of habitat and resource availability (conservation biological control) (DeBach and Rosen 1991; van Driesche and Bellows 1996; Orr & Suh 2000)

i) Importation

It is not unusual for a pest species to be accidentally introduced into a new area or for a species that poses no threat in its home environment to become invasive when introduced into a new location (van Lenteren 1995). Such a species can, in the absence of natural enemies, easily proliferate and achieve pest status. If local predators or parasites are unable to exploit a foreign species, it may be necessary to import an exotic natural enemy (see reviews in DeBach and Rosen 1991; van Driesche and Bellows 1996; Orr & Suh 2000). The control agent selected is normally associated with the pest in its home range, but this is not imperative. A species that normally attacks a close relative of the target organism can also be effective in the absence of a specific natural enemy (Carl 1982). The relative merits of new versus old natural enemy associations have prompted a contentious debate (Hokkanen & Pimentel 1984; Waage & Greathead 1988) and are discussed further in Chapter 2.

Importation, or 'classical' biological control, carries the advantage that it requires no maintenance after the initial introduction. However, its rate of success has been both emphasised (e.g., Carruthers & Onsager 1993; van Driesche & Bellows 1996) and challenged (Hall *et al.* 1980; Gurr & Wratten 1999; Gurr, Barlow *et al.* 2000).

ii) Augmentation

Augmentation of natural enemies may be necessary when populations are absent from a certain area (e.g., glasshouses), late to colonise newly-planted crops, or simply present at densities that are too low to allow successful biological control (for reviews of augmentation of biological control see Rabb *et al.* 1976; Ridgway & Vinson 1977; van Lenteren 1986; DeBach and Rosen 1991; van Driesche and Bellows 1996; Orr & Suh 2000).

There are a number of ways in which natural enemy populations can be augmented. Inoculative releases involve the release of natural enemies early in the crop cycle so that their offspring and late-arriving individuals will subsequently suppress pest populations. This approach has been applied in a variety of situations such as predaceous mites with poor natural rates of dispersal (Huffaker & Kennett 1956) and glasshouse releases of aphid parasitoids (Starý 1993). Conversely, inundative releases involve the application of natural enemies in a similar manner to pesticides (reviewed in Rabb *et al*. 1976). Whether the control agent is sprayed on (pathogens and nematodes) or mass released (predators and parasitoids), *in situ* reproduction of the natural enemy is unnecessary. Only those individuals that are released are required to provide control, as periodic re-releases ensure high population densities.

iii) Conservation Biological Control

Attention has focused recently on the indirect enhancement of both endemic and introduced natural enemies through habitat management (Barbosa 1998; Pickett & Bugg 1998; Gurr & Wratten 1999, Letourneau & Altieri, 1999; Gurr & Wratten *et al.* 2000; Landis *et al.* 2000, Orr & Suh 2000). The basic premise of this technique is that agricultural systems are ecologically depauperate environments that can be unfavourable to natural enemies. There are two major elements to natural enemy enhancement via conservation biological control. First, a reduction in quantity or a change in the type or timing of pesticide application can enhance natural enemy survival (Settle *et al.* 1996; Ruberson *et al.* 1998). Second, provision of resources that are absent from the crop system can enhance natural enemy survival/efficacy.

A number of studies have demonstrated that non-crop resources enhance one or more components of natural enemy fitness (e.g., Andow & Risch 1985; Jervis *et al.* 1993; Hickman *et al.* 1995; Dyer & Landis 1996; Irvin *et al*. 2000; Johanowicz & Mitchell 2000; Berndt *et al.* 2001; Sagarra *et al*. 2001), and alter the spatial distribution of natural enemies (Lövei *et al.* 1992; Liang & Huang 1994). However, few studies have both explored the effects of resource subsidies on natural enemies in the field and tested the mechanisms underlying these effects (Berndt *et al.* 2001). The mechanistic effects of floral resource subsidies on parasitoid fitness and efficacy are the subject of this thesis.

BIOLOGICAL CONTROL OF CEREAL PESTS IN NEW ZEALAND

Cereals are culturally and economically important as primary global food crops. One hundred and fifty thousand ha of cereals are grown in New Zealand, producing an annual income of between $3.0m (1997) and $6.8m (2001) (New Zealand Ministry of Foreign Affairs & Trade 2001). Possibly the greatest amount of damage sustained by cereal crops in New Zealand is caused by aphids. Aphid feeding can cause significant physical damage to cereals, particularly during early growth stages (Watt & Wratten 1984; Pike & Schaffner 1985; Kieckhefer & Gellner 1992), aphid honeydew can hinder photosynthesis and promote growth of saprophytic fungi (Rabbinge *et al.* 1981), and aphids are the sole vector for the spread of barley yellow dwarf virus (BYDV), the most serious disease affecting wheat in New Zealand (Smith 1963).

Effective chemical control of cereal aphids in New Zealand is estimated to cost between $3.6 - $5 million per year, a very expensive alternative to biological control (Grundy 1989). Several species of parasitoids have been imported into New Zealand for aphid control, and habitat manipulation to enhance aphid predation by, for example, hoverflies has also been examined (Hickman *et al*. 1995; Wratten *et al.* 1995).

When examining fundamental ecological problems, aphids have several practical advantages over other insect herbivores as model organisms, such as their short generation times, ease of culturing and ease of manipulation in the field (Müller and Godfray 1999). Aphids are also major economic pests, causing damage to a variety of food and ornamental crops worldwide (Wellings *et al*. 1989).

This thesis focuses on a system involving wheat *Triticum aestivum* (L.) (Gramineae), the parasitoid *Aphidius rhopalosiphi* De Stefani-Perez (Hymenoptera: Aphidiidae) and one of its hosts, the rose-grain aphid *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae), a major pest of wheat in New Zealand. The plant selected to provide resource subsidies is buckwheat *Fagopyrum esculentum* Moench (Polygonaceae). It has been used for this purpose previously because it has open, exposed nectaries, allowing easy access by insects (Berndt *et al*. 2001). Buckwheat is also inexpensive and requires little maintenance, making it a candidate for general use by biological control practitioners.

Aphidius rhopalosiphi

The Aphidiidae (Hymenoptera: Ichneumonoidea) contains more than 400 species within approximately 60 genera and subgenera (Starý 1970, 1988). They are closely related to, and sometimes even included as a subfamily of the Braconidae (Mackauer & Starý 1967). All species within the Aphidiidae are solitary endoparasites of ovoviviparous aphids and are therefore potentially useful for aphid biocontrol. Because of this potential utility, the foraging strategies and population dynamics of aphidiid parasitoids have received considerable attention (Gardner & Dixon 1985; Stadler & Völkl 1991; Völkl 1994a; Mackauer *et al.* 1996; Jarosik & Lapchin 2001).

Starý (1988) provides an excellent review on the biology and oviposition behaviour of aphidiid parasitoids, and Gardner (1982) provides ecological and behavioural information specific to *A. rhopalosiphi*. Starý (1970) provides a key to the genera and subgenera of aphid parasitoids of the world, Powell (1982) and Pike *et al.* (1997) provide keys to British and North American species of cereal aphid parasitoids and Pungerl (1986) provides an excellent key to species of *Aphidius* Nees.

Briefly, the features that allow *A. rhopalosiphi* females to be distinguished from other species of *Aphidius* parasitising cereal aphids include: i) the presence of a metacarpus wing vein, ii) between 6 and 19 fine grooves or ‘costulae’ on the anterolateral area of the first metasomal tergum, iii) no extended second valvula of the ovipositor, iv) maxillary palps four-segmented and v) antennae 16 – 18 segmented (Pungerl 1986) (Fig. 1). The characters

used for identification of aphidiid parasitoids are applicable only to females, therefore the taxonomic identity of males can only be assured for captively-reared individuals.

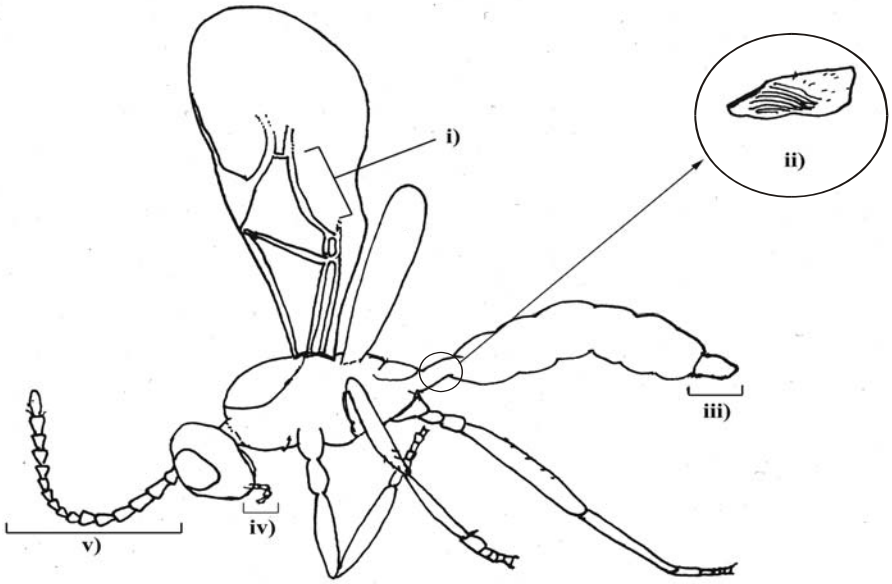

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Figure 1: Diagram of *Aphidius rhopalosiphi* showing features used for identification: i) Metacarpus present, ii) first metasomal tergum with 6-19 costulae, iii) second valvula of ovipositor normal (i.e. not markedly elongate), iv) maxillary palps four-segmented, and v) antennae 16-18 segments. Characters for identification following Pungerl (1986).

Metopolophium dirhodum

The genus *Metopolophium* Mordvilko (Aphidinae: Macrosiphini) contains approximately 18 species that superficially resemble *Acyrthosiphon*, but are more closely related to *Sitobion* (Blackman & Eastop 2000). In common with other species of *Metopolophium* and *Sitobion*, *M. dirhodum* is associated with Gramineae (its secondary hosts); however, the primary hosts of this species are wild and cultivated *Rosa* spp. (Rosaceae).

M. dirhodum is a heteroecious, predominantly leaf-feeding species found on numerous grasses and cereals. Adult apterae are laterally compressed, green or yellowish-green in colour and possess a brighter green longitudinal dorsal stripe. Full descriptions of

this and related species are provided by Scott (1984) and Blackman & Eastop (2000), and a key for identification of common small grain aphids is provided by Olsen *et al.* (1993).

Metopolophium dirhodum was first found in New Zealand in 1981. It infests a variety of grain crops, potentially causing an annual loss of yield of between $1m and $20m in New Zealand alone (Grundy 1989). In addition, *M. dirhodum* can act as a vector for BYDV (Waterhouse *et al*. 1985), which causes stunting and discolouration of crops and sometimes a dramatic reduction in yield (Smith, 1963).

Aphidius rhopalosiphi was originally introduced into New Zealand as a biological control agent of *M. dirhodum*. It was selected as a potential agent because it was found to be the most frequently occurring parasitoid of *M. dirhodum* in Southern England (Dean *et al.* 1981). Cultures originating from France and England were received in autumn 1985 and released throughout New Zealand between 1985 and 1987 (Grundy 1989). Rates of *M. dirhodum* parasitism by *A. rhopalosiphi* in New Zealand appear to be on the order of 40 – 100 % depending on the season (Farrell & Stufkens 1990), making the cost to benefit ratio for this introduction favourable (Grundy 1989). Although it was introduced only to control *M. dirhodum*, *A. rhopalosiphi* has a relatively broad range of accepted host species, including *Sitobion avenae* (F.) (Pungerl 1986; Hoeller 1991), *M. festucae* Stroyan*, Diuraphis muehlei* Borner (Hoeller 1991), *S. fragariae* Walker, *Rhopalosiphum padi* (L.), *R. maidis* (Fitch) and *Myzus persicae* (Sulzer) (Farrell & Stufkens 1990).

AIM AND OUTLINE OF THESIS

The broad aim of this thesis was to examine how biological control of *M. dirhodum* by *A. rhopalosiphi* can be enhanced by floral resource subsidies, and the mechanisms underlying this enhancement. Chapter 2 examines the role theoretical ecology has played in biological control, as well as fields of ecology that may make further contributions. In particular, emphasis is placed on habitat manipulation, resource subsidies and criteria for successful implementation of a biological control programme.

Chapter 3 describes laboratory experiments that examine mechanisms by which *A. rhopalosiphi* may exhibit enhanced fitness from floral resource subsidies. These experiments

measure only potential fecundity in the form of egg load and longevity. Realised fecundity, in the form of enhanced rates of parasitism, is the focus of Chapter 4.

Chapter 4 describes field and laboratory experiments that measure the combined effect of floral resources on parasitoid fecundity and rates of parasitism. These experiments test whether the mechanisms established in Chapter 3 operate under field conditions with variable biotic and abiotic influences. Effects of floral resources on aggregation, mate encounter rates and rates of predation on parasitoids combine with effects on fecundity, providing a more realistic understanding of how floral resources affect the biological control of *M. dirhodum* by *A. rhopalosiphi*.

Chapter 5 provides a general discussion of the results in Chapters 3 and 4, placing them in the context of the ecological theory presented in Chapter 2. Chapter 5 presents conclusions on resource subsidies and their importance to biological control, and highlights significant gaps in current knowledge that require future research.

CHAPTER 2: ECOLOGICAL THEORY FOR BIOLOGICAL CONTROL

INTRODUCTION

The use of insect natural enemies for biological control is not a recent concept. Preliminary introductions were made as early as the late nineteenth century although they showed little regard for the ecological consequences of species invasions (for a review of the origins of biological control, see DeBach & Rosen 1991; Tscharntke & Kruess 1999). Remarkably, despite improved screening, selection and testing procedures, the success rate of control agents today differs little from that of the earliest introductions. Continuing low success rates do not appear to be related to the establishment of the agent, as the percentage of introduced species becoming established has increased in recent years (Greathead & Greathead 1992; Gurr & Wratten 1999, Gurr, Barlow *et al.* 2000). With no net improvement in classical techniques, attention is now shifting towards the use of ecological theory to find a means of augmenting success rates (Mackauer *et al.* 1990; Waage 1990; DeBach & Rosen 1991; Ehler 1994; Sheehan 1994; Barbosa 1998; Wratten *et al.* 1998; Berryman 1999; Gurr & Wratten 1999; Hawkins & Cornell 1999; Landis *et al.* 2000). However, a conceptual divide exists between ecological theory and practical agriculture. Although classical biological control has contributed to the theory of insect population ecology (for examples see Kareiva 1996), there is little evidence that this contribution has been reciprocated (Waage 1990; Kareiva 1996 but see Murdoch & Briggs 1996; Fagan *et al.* 2002). Despite the move to integrate ecology and biological control, workers often use different terminology for similar concepts.

The aim of this review is to examine the areas of ecology that have already made a contribution to biological control and to highlight new areas that have not yet been viewed in this context. Food web theory in particular may be beneficial to the ongoing search for improved biological control techniques. A seminal paper by Waage (1990) examined how ecological theory relates to the selection of biological control agents. Research subsequent to that paper will be reviewed here to determine how ecology has further contributed to the scientific process of agent selection. This chapter will not discuss parasitoid aggregation,

population stability, refuge size or density dependence as these areas have been recently reviewed (Murdoch & Briggs 1996). A pragmatic approach will be taken by outlining the steps involved in implementing a biological control programme and then describing how ecological theory can be incorporated into host and habitat manipulation to enhance natural enemy success. The aim is to provide a synthesis of ecological and agricultural terminology (Table 2.1), so that future studies in ecology and biological control are less likely to be hampered by a confusion of concepts and a lack of communication.

IMPLEMENTING A BIOLOGICAL CONTROL PROGRAMME

Several processes should ideally be incorporated into a classical biological control programme (DeBach & Rosen 1991; Kidd & Jervis 1996; van Driesche & Bellows 1996; van Driesche & Hoddle 2000). The first is an evaluation of the identity, distribution and abundance of the pest in its target location (Kidd & Jervis 1996; van Driesche & Bellows 1996). Correct identification is imperative, as control agents may be highly host- or habitat-specific. The distribution and abundance of a pest can also affect the choice of agent and its effectiveness after release.

The second step requires the location of a natural enemy or enemy complex. The search for natural enemies usually begins in the areas of origin of the pest. A sense of urgency to find an agent quickly, limited funding, and a need for a species that can be easily cultured, often result in the selection of sub-optimal control agents (Waage 1990). Areas of local pest outbreaks are frequently sought as a source of natural enemies, although high pest density may imply weak control by existing enemies (Pschorn-Walcher 1977; Fuester *et al.* 1983; Waage 1990). Therefore, sampling areas of low pest density, although more difficult, may be a preferable means of selecting agents (Waage 1990).

The decision to use a predator or parasitoid usually associated with the pest or to use an entirely new agent (either from a different habitat or one that uses a host closely related to the pest) lacks conclusive guidance from ecological theory (Kidd & Jervis 1996). Waage and Greathead (1988) found no significant difference between new and old associations in their relative success rates. Hokkanen and Pimentel (1984, 1989), however, maintained that evolved commensalism is absent from new associations and that this results

in “more virulent exploiters” for biological control. Waage (1990) demonstrated that new associations can be as effective as old ones, provided the natural enemy is already established, although establishment itself can be a difficult process. Consideration of ecological theory is essential when evaluating a potential new association, as there are no previous successes or failures to provide species specific empirical information. However, examination of a related species of pest and control agent may provide an insight as to how a natural enemy may respond after introduction to a new environment.

Knowledge of the phylogeny and ecology of new natural enemies is imperative before they can be released, both to improve their success rate and to reduce the risk of environmental harm (Simberloff & Stiling 1996; Strand & Orycki 1996; Berryman 1999; Gurr & Wratten 1999; Landis *et al.* 2000; Hopper 2001; Strong & Pemberton 2001). Theoretical criteria (based on life-history characteristics, community ecology and phylogeny) can help to determine the relative merits of different natural enemies before they are introduced (Waage 1990; Strand & Obrycki 1996). Models based on laboratory experiments can be used to examine the theoretical benefits of a new agent before its introduction (Beddington, Free & Lawton 1978), however, these models have been criticised as of limited value because of their simplicity and their reliance on assumptions (Putman & Wratten 1984, Guttierrez *et al.* 1994; Barlow 1999).

The Type of Agent Used

Different biological control agents have different advantages. Characteristics of a natural enemy’s life-history and distribution, as well as the structure of, and resources within the target landscape should ideally be considered prior to any biological control introduction. For example, host ranges of parasitoids tend to be narrow, with most species parasitising only one or a few hosts, whereas predators are usually more polyphagous. Synchrony of parasitoid emergence with particular host life-history stages or generations can facilitate high attack rates, thereby making the agent more effective (Beddington *et al*. 1978; Phillips *et al.* 2001). Although promoted as one of the benefits of biological, compared with chemical pest control, the importance of specificity may have been

overestimated by biological control workers (Strand & Obrycki 1996). Host or prey shifts can occur in control agents (Hokkanen & Pimentel 1989; van Emden 1990; DeBach & Rosen 1991; Secord & Kareiva 1996; Strand & Obrycki 1996) in the same way that host plant shifts occur in herbivorous insects (Gould 1979; Carrol & Boyd 1992). Higher host specificity in parasitoids can even promote host shifting by exerting stronger directional selection than a generalist or non-parasitic life history. The host itself is the parasitoid larval environment and in the absence of an ideal host, a parasite lineage must adapt or die (Secord & Kareiva 1996). Host shifts or host-range expansions can pose a great environmental risk, and at the very least can render the control agent ineffective.

The local environment also places some restrictions on the suitability of certain control agents, although some environmental constraints can be alleviated with spatial subsidies (Landis *et al.* 2000; Table 2.1). Plant and landscape structure may play an important role in biological control interactions, and can be manipulated to some extent in agroecosystems. Plant structures, such as domatia, trichomes and epidermal waxes can provide a refuge for phytophagous arthropods, reducing mortality from predation and parasitism (Gardner & Dixon 1985; Arditi & Ginzburg, 1989; Hawkins 1993; van Driesche & Bellows 1996; Barbosa & Wratten 1998). Plant structure can also be used or manipulated by the insect for its own defence, by inducing gall formation, or by burrowing into leaves and stems (Hawkins 1990; Godfray 1994; van Driesche & Bellows 1996). Parasitoids to be used as biological control agents should therefore be selected for a host-searching behaviour that is effective on the host plant of the target pest species (Gardner & Dixon 1985; Patt *et al.* 1997a; Agrawal & Colfer 2000; Gingras *et al*. 2002). Plants may even manipulate natural enemies in order to reduce herbivore damage. This manipulation may involve structural modifications that improve accessibility or survival of predators and parasitoids (Marquis & Whelan 1996; Norton *et al*. 2001) or infochemical modifications whereby natural enemies are attracted by host plant volatiles released during herbivore feeding (e.g., Havill & Raffa 2000; Shiojiri *et* al. 2001).

Landscape structure (and its effect on host distribution) can also affect parasitism rates (Hassell & Pacala 1990; Marino & Landis 1996; Roland & Taylor 1997; Tscharntke & Kruess 1999), with populations of patchily distributed hosts being reduced more

successfully by parasitoids showing aggregative responses (Beddington *et al*. 1978). However, some of the studies showing an effect of landscape structure on rates of parasitism failed to replicate landscape complexity adequately, making it uncertain whether the effect is consistent across different landscapes (Menalled *et al*. 1999). Landscape structure can also influence predation by affecting movement and aggregation of beetles (Crist & Wiens 1995; Frampton *et al*. 1995; Mauremootoo *et al.* 1995; With & Crist 1995; Wiens *et al.* 1997) and hover flies (Wratten, Bowie *et al.* in press) across different landscape types. The implications of this are probably of general importance for all biological control agents, and serve to highlight the effect of spatial arrangement of crop and non-crop plants. Research in this area may provide explanations for the relative success or failure of predators in different habitats.

How Many Species of Agent?

Many biological control introductions involve only one species of agent. This is probably an economic decision (and safer in terms of potential side effects; e.g. Howarth 1991, 2000). However, the introduction of more than one species may prove to be more successful. The ecological theory surrounding guild structure (e.g., Hawkins & MacMahon 1989), intraguild competition (e.g., Ehler & Hall 1982; Mills 1992, 1994) and intraguild predation (e.g., Polis & Holt 1992) can provide an insight into the advantages or disadvantages of several agents over just one, by explaining how members of a guild may interact with one another. If members of a guild can act as complementary sources of host/prey mortality (e.g., Goldson *et al.* 1994) they could prove to be very useful in biological control. If, however, competitive interactions inhibit the effectiveness of one or more guild members (e.g., Raymond *et al.* 2000), a strategy of introducing only one species of agent may provide the optimal level of pest control.

GUILD STRUCTURE

The term ‘guild’, as defined by Root (1967) refers to “a group of species that exploit the same class of environmental resources in a similar way” (Table 2.1). This classification is based on ecology rather than phylogeny, and can be used to describe

groups of biological control agents exploiting the same host/prey (Miller & Ehler 1990; Mills 1994) or, more specifically, a given stage of the host (Ehler 1992). The classification of Ehler (1992), in which the organisms exploit a particular 'resource unit' or developmental stage of a given host species, has also been termed a 'component guild' (Miller & Ehler 1990). Many parasitoids attack only one developmental host stage (Godfray 1994), so component guilds containing just one species each will result in less niche overlap (and less intraguild competition) than if many members of the guild occupy the same component guild, as is the case with many generalist predators.

The structure and function of a parasitoid guild can be affected by habitat structure (Roland & Taylor 1997) and stability (Force 1974; Miller 1980), intraspecific and interspecific competition (Ehler & Hall 1982, Tallamy 1983; Mills 1992, 1994), and host density (Ehler 1992). The responses of individual species within the guild to these factors may vary (Roland & Taylor 1997), allowing one species to compensate for a reduction in the performance of another (Matsuda *et al.* 1993). When parasitoids are exerting a level of control close to their maximum potential (indicated by strong density dependence and multispecies exploitation of most host patches), disruptive use of insecticides should be avoided, whereas the reverse pattern may indicate that immediate intervention (such as the application of pesticides) is necessary (Miller & Ehler 1990). Studies of parasitoid species associated with the gall midge *Rhopalomyia californica* (Diptera: Cecidomyiidae) revealed that the number of constituent species within the guild influenced its effectiveness to a greater degree than the density of individuals within each species (Ehler 1992). Guild structure can theoretically be altered to increase the impact of the guild on the target pest population (Ehler 1992).

Assembly and establishment of a parasitoid guild must be consistent with the target habitat and flexible enough to allow guild restructuring (e.g., by inundative release of certain species) as conditions change (Miller & Ehler 1990). Natural enemy complexes (the various guilds of parasites, predators and pathogens) add a higher level of complexity to the practice of biological control. Different guilds can be used to attack different life history stages of the pest, or to augment each other. For example, a parasitoid may also act as a vector for a microbial pathogen (Weiser *et al.* 1976; Begon *et al*. 1999). Ecological models

relating to population biology can be modified to investigate insect-pathogen interactions (Godfray & Briggs 1999) and host-pathogen-parasitoid interactions (Begon *et al.* 1999), providing an important framework for field and laboratory studies.

INTRAGUILD COMPETITION

Intraguild competition may inhibit the establishment of new parasitoids introduced into an area containing species that already occupy a similar niche (Ehler & Hall 1982; Tallamy 1983; Mills 1992, 1994; Janssen *et al.* 1998 but see Keller 1984; Murdoch *et al.* 1996; van Emden 1990; Bogran *et al.* 2002). Alternatively, newly introduced parasitoids may augment the impact of established species and increase host suppression (Goldson *et al.* 1994). Force (1974) compared rates of parasitism by six parasitoid species in isolation and in several mixtures. In some cases parasitism rates were higher in mixed treatments than in treatments containing only one of the constituent species, whereas in some cases the reverse pattern was observed. This suggests that intraguild competition may be largely case-specific, however intraguild theory provides predictions about the probability of competition between members of a natural enemy guild.

Competition for host larval resources results in strong intraspecific and interspecific interactions within parasitoid communities (Mills 1992, 1994). Although different species of parasitoid may attack different host stages from different feeding sites, ultimately each individual host is capable of sustaining only a limited parasitoid load. Knowledge of guild theory is especially important for selection of natural enemy complexes that will exhibit lower intraguild competition than would otherwise arise from an overlap in host preference (Ehler & Hall 1982, Tallamy 1983; Mills 1992, 1994). An extreme form of this competition is multiparasitism, where larvae of two species of parasitoids compete for the resources of one host individual (Godfray 1994). Koinobiont parasitoids (that allow the host to continue to grow after parasitism) are more susceptible to intraguild competition as the host (and parasitoid larva) remains vulnerable to other parasitoids that specialise on later host life-stages. Conversely, idiobionts (where the parasitoid utilises only the host resources present at oviposition) remove the opportunity for specialists of later life stages to oviposit, as the host will never develop any further. In

selecting a suite of control agents, then, it would be preferable to exclude hyperparasitoids from a guild and if possible include only idiobionts that specialise on different host life-stages. This would eliminate the possibility of direct larval competition within the host. However, those idiobionts that specialise on the earliest host life-stage will still gain a competitive advantage by removing host resources from parasitoids that attack later life stages.

Competition between members of a guild need not always be interspecific. In a study of competition among coccinellid beetle larvae, Evans (1991) found no significant difference between conspecifically and heterospecifically reared individuals in terms of larval weight gain, or the reduction of aphid prey populations. If intraspecific competition is generally as important as interspecific competition, then introduction of a new natural enemy that exploits the pest in a different way may reduce overall control agent competition, when compared with only one species of agent.

Apparent competition, whereby two hosts that do not normally compete for resources interact via a shared natural enemy, may also affect biological control introductions. The aggregative and switching effects of two species of hosts in different habitats can promote persistence and stability of one-parasitoid-two-host interactions (Bonsall & Hassell 1999). However, apparent competition between parasitoids via a shared hyperparasitoid may negatively affect biological control, either by reducing numbers of one of the parasitoid species (van Nouhuys & Hanski 2000), or through behavioural effects of hyperparasitoids increasing herbivore reproductive rates (Boenisch *et al*. 1997; van Veen *et al.* 2001). Unfortunately, despite its potential importance, testing for apparent competition may be difficult and the possibility of direct competition can not always be excluded (Morris *et al*. 2001).

INTRAGUILD PREDATION

Direct non-competitive interactions such as inter- or intraguild predation can also affect the degree of control exerted on a target pest. In a study of potential agents for the control of stored product insects, Press *et al.* (1974) found that the predaceous bug *Xylocoris flavipes* preyed on at least one life-stage of the parasitic wasp *Bracon hebetor*, so

that the effectiveness of these two control agents combined was less than that of *B. hebetor* alone.

It is important to distinguish intraguild predation (IGP) from competition because the intraguild predator gains an immediate energy benefit from feeding (e.g., hyperparasitism, where a second parasitoid species feeds not on the host, but on another parasitoid larva; Sullivan 1987; Godfray 1994; Sullivan & Völkl 1999). However, IGP differs from classical predation because the prey is also a potential competitor, so the predator also gains a competitive advantage (Polis & Holt 1992). Intraguild predation is more likely when generalist predators are used as biological control agents, because they can consume other control agents as well as the target pest (Janssen *et al.* 1998). This can alter dynamic stability or lead to exclusion of the intraguild predator or other predator species i.e., the predator's intraguild prey (Holt & Polis 1997). Adding a new natural enemy that can prey on members of its own guild can have indirect effects on prey, potentially leading to an undesirable increase in pest populations (Rosenheim *et al*. 1993; Janssen *et al.* 1998; Merfield *et al.* in press).

HABITAT MANIPULATION TO ENHANCE BIOLOGICAL CONTROL

Like all organisms, predators and parasites are affected by a suite of biotic and abiotic factors. Manipulation of these factors to enhance the effectiveness of biological control agents is a focus of 'conservation biological control', a subject that has received considerable attention in recent years (Kidd & Jervis 1996; Barbosa 1998; Wratten *et al.* 1998; Gurr & Wratten 1999; Gurr, Wratten *et al.* 2000). The ecological literature has examined mechanisms that may enhance predator and parasitoid effectiveness (e.g., Gardner & Dixon 1985; Hawkins 1992, 1993; Polis & Strong 1996), although these mechanisms have not always been incorporated into the biological control literature. Conservation biological control provides an appropriate link between these disciplines. Areas of ecological theory that are relevant to conservation biological control will now be examined. Emphasis will be placed on food web theory, as it helps to explain the mechanisms underlying control agent enhancement.

Food-Webs: Turning top-down control on its head

The classical predator/prey models (e.g. Lotka-Voltera and Nicholson-Bailey) assume that even though prey abundance affects predator abundance, predators still have a significant impact on prey populations; i.e., natural enemies exert "top-down" (recipient) control. The alternative, "bottom-up" (donor) control, whereby plants limit herbivore populations and the regulatory effects of predators are minimal or absent, has previously received little attention (with the exception of aquatic systems e.g. McQueen *et al.* 1989) or has been assumed to be rare (e.g. Arditi and Ginzburg 1989).

Current understanding of food-web complexity, however, challenges the concept of strong recipient control across discrete 'trophic levels'. The theory relating to systems previously thought to be under recipient control has come into question (Menge & Sutherland 1987; Hawkins 1992; Polis & Strong 1996), while evidence that bottom-up control is a powerful structuring force has emerged (Edwards *et al.* 1991; Hawkins *et al.* 1997; Hodge *et al.* 1999). Trophic level integrity is necessary for recipient control, as the ecosystem is considered to be structured entirely by the relative abundance of consumers at each trophic level. However, processes such as omnivory, cannibalism and intraguild predation (including facultative hyperparasitism) diffuse the flow of resources across the trophic spectrum, rather than localising production and consumption at certain trophic levels (Menge & Sutherland 1987; Hawkins 1992; Polis & Strong 1996). These processes serve to increase consumer abundance, but because feeding is dispersed across the trophic spectrum, consumption is not concentrated enough to impose the powerful structuring force required for top-down control. Simple predator/prey or parasite/host models do not, therefore, describe natural enemy ecology adequately (Barlow 1999), as interactions with non-host or non-prey species are overlooked.

Agricultural systems are ecologically impoverished, representing a subset of organisms that benefit humans, while minimising (either manually or chemically) populations of organisms such as pests, or those that have no perceived value (Aebischer 1991). Classical biological control has assumed that the presence of only the target host or prey species is sufficient to maintain a control agent population capable of reducing pest density. This is generally not the case, as resources other than the target pest are required by

the control agent and may be absent from the crop ecosystem (see sections on life-history omnivory and shelter and microclimate below). In the absence of these non-host/prey resources, predator/parasitoid populations may not be able to achieve the threshold density necessary for successful top-down control (Gardner & Dixon 1985; Hawkins 1992, 1993; Polis & Strong 1996).

If crop plants limit herbivore population densities, which in turn limit the predator/parasitoid population (as described above) bottom-up, rather than top-down control appears to be the dominant structuring force in agricultural systems. This may be one of the reasons why the success rate of classical biological control is relatively low, despite many introductions of agents that have established (Hall *et* al. 1980; Greathead & Greathead 1992; Gurr & Wratten 1999). How, then, can food web theory be incorporated into biological control programmes to increase the degree of top-down control?

The difficulty of using natural enemies for biological control if bottom-up control drives food web dynamics can be overcome when predators/parasitoids receive a resource subsidy in addition to the host/prey. Polis & Strong (1996) used the term "spatial subsidies" (Table 2.1) to describe the process of obtaining resources from outside the target habitat. However, in agricultural systems non-crop resources may occur within or beyond the crop boundary, so the term 'resource subsidy' better describes a process analogous to spatial subsidies within or adjacent to the target habitat.

Life-history omnivory (feeding at different trophic levels during different life stages), combined with resource subsidies, allows an increase in predator/parasitoid abundance beyond that which the pest population can support on its own (Polis & Strong 1996). Predator or parasitoid population dynamics can therefore be uncoupled from the population dynamics of the pest species, leading to high densities of the control agent, even at low pest densities (Hawkins 1992, 1993). These high densities achieve a similar result to natural enemy augmentation (see Chapter 1).

Food web engineering based on the principles of life-history omnivory and resource subsidies has been applied to agriculture for thousands of years. Berenbaum (1996) lists Pliny the Elder (AD 23-79) as discussing intercropping to reduce insect attack, and recently the discipline of conservation biological control has revived interest in

'companion planting'. Although some biological control studies (e.g. Gurr, van Emden & Wratten 1998) have attempted to draw on the ecological literature to understand the mechanisms promoting natural enemy success, the majority has relied on empirical observation. Nonetheless, several fundamental ecological principles underlie these practices, including the relationship between diversity and food web stability, life-history omnivory and refuges.

THE EFFECTS OF PLANT SPECIES DIVERSITY

The impact of species diversity on food web stability and ecosystem function has inspired a long running debate in ecology (Lawton 1994; Naeem *et al.* 1994; Hanski 1997; Huston 1997; Naeem & Li 1997; Tilman *et al.* 1997; Bengtsson 1998; Naeem 2000; Tilman 2000; Wardle *et al.* 2000). Whether increasing plant species diversity can be used to enhance biological control has also prompted debate. In agricultural systems, diversity can be manipulated relatively easily by removing weeds, by adding non-crop plants or by intercropping (Risch *et al.* 1983). Increasing diversity through intercropping may or may not reduce pest populations (Risch *et al.* 1983; Andow & Risch 1985; Andow 1991), and the mechanisms that determine how herbivores will respond to plant diversification are not always obvious (reviewed in Wratten, Gurr *et al*. in press). Root (1973) proposed two hypotheses for the observed differences in herbivore abundance between diversified and non-diversified systems. The predation or 'enemies' hypothesis predicts that populations of natural enemies will be enhanced by floral resources, shelter or alternative hosts/prey, and that this will lead to lower herbivore population densities (Root 1973). This is essentially the same argument used to explain the effects of spatial subsidies on natural enemies (Polis & Strong 1996). Root's 'resource concentration' hypothesis predicts that host-specific herbivores will tend to find their host plant species more easily, and thus aggregate more readily, in areas of host-plant concentration such as monocultures. These hypotheses are basically assessments of the relative importance of top down vs. bottom-up control on herbivore populations, but the empirical evidence for which mechanism dominates is variable (Russell 1989; Andow 1991; Wratten & van Emden. 1995; Hooks & Johnson 2001). Diversity-induced changes in herbivore movement have been used as evidence for

the resource concentration hypothesis (Risch *et al.* 1983; Hodge *et al.* 1999). However, natural enemies can also theoretically limit herbivore populations more efficiently in diverse systems (Sheehan 1986). Conversely, Andow & Risch (1985) found that predator density may be lower in polycultures than in monocultures, although reduced predator density does not always imply reduced control, as per capita efficacy of predators may be improved by floral resource subsidies. It is important to note that the two hypotheses are not mutually exclusive, as top-down and bottom-up effects on herbivores can be exerted simultaneously (Rosenheim 1998; Williams *et al*. 2001). However, which hypothesis better explains observed herbivore responses to plant diversification and the circumstances under which natural enemies and resource concentration will act complementarily, independently or antagonistically remains to be determined (Andow 1991).

Many authors have noted that diversity *per se* may not be as important in natural enemy enhancement as the particular attributes of habitat structure or the plant and animal species that make up that diversity (van Emden 1990; Kidd & Jervis 1996; Gurr *et al.* 1998; Wratten, Gurr *et al*. in press). It is these specific attributes (such as alternative foods or shelter) that may be of greater value in this context, as increasing diversity *per se* can have negative effects such as an increase in pest numbers (Risch *et al.* 1983; Kidd & Jervis 1996; Baggen & Gurr 1998; Gurr *et al.* 1998), a loss of productive land area, or the risk of plants becoming invasive in the future (Kidd & Jervis 1996). The mechanisms responsible for the enhancement of natural enemy success through increased plant diversity will now be examined.

LIFE-HISTORY OMNIVORY

Although host-feeding occurs in some parasitoids (Jervis & Kidd 1986), many use the host only for oviposition and larval development, requiring nutrients from other sources during their adult life (see reviews in Jervis *et al.* 1993 and Jervis & Kidd 1996, 1999). If the resources necessary for the survival of one particular life-history stage are absent, an "ontogenetic bottleneck" (Werner & Gilliam 1984) can limit further development (Polis & Strong 1996). Sugars (e.g., from floral and extrafloral nectaries or aphid honeydew) can enhance parasitoid longevity (Arthur 1944; Dyer & Landis 1996; Heimpel *et al.* 1997;

Jacob & Evans 2000; Johanowicz & Mitchell 2000; Rosenheim *et al.* 2000; Sagarra *et al*. 2001) and fecundity (Singh, Singh *et al.* 2000) and pollen can provide an important protein source for females approaching sexual maturity (Andow & Risch 1985; Jervis *et al.* 1993; Hickman *et al.* 1995, Wheeler 1996; Irvin *et al.* 2000). When sufficient resources do not occur naturally within or near the crop, these requirements can be met with resource subsidies in the form of managed floral strips (Hickman & Wratten 1996; Gurr *et al.* 1998; Stephens *et al.* 1998; Wratten et al., 1998; Landis *et al.* 2000). If the natural enemies disperse slowly, positioning the floral strips within the crop may be particularly useful. Such strips must contain plants with a floral architecture that is compatible with the morphology and foraging behaviour of the target biological control agent (Gilbert 1985; Patt *et al*. 1997a, b) and, ideally be unavailable to the target pest (Baggen & Gurr 1998).

Honeydew produced by aphids when added to alfalfa attracts large numbers of predators and parasitoids of the alfalfa weevil (Evans & England 1996). This example not only demonstrates the value of resource subsidies (in this case honeydew) to natural enemies, but also possible intraguild competition amongst herbivores. In this example the aphids may derive a competitive advantage over the weevils via the indirect effect of their honeydew on weevil natural enemies.

Resource subsidies can also be important for rapid colonisation of annual crops by natural enemies. This is especially true when the subsidy comes in the form of alternative hosts or prey, which can maintain predator or parasitoid populations inside or outside the crop, allowing rapid colonisation of the field when pests become established (van Emden 1990; Corbett & Rosenheim 1996; Settle *et al.* 1996; Landis *et al.* 2000). For example, the parasitoid *Lysiphlebus testaceipes* (Hymenoptera: Aphidiidae) can maintain itself on the alternative host *Aphis helianthi* (Homoptera: Aphididae) on sunflowers when the pest *Schizaphis graminum* (Homoptera: Aphididae) is rare or absent from the sorghum crop (Powell 1986 cited in van Emden 1990). The presence of alternative hosts may also prevent facultatively hyperparasitic species from parasitising other members of their guild.

Although alternative hosts can be important in maintaining populations of parasitoids, it does not necessarily follow that these parasitoids will always return to using the pest species as a host. Cameron *et al.* (1984) showed that when a population of the

parasitoid *Aphidius ervi* (Hymenoptera: Aphidiidae) was maintained on pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae) populations outside the crop field, the parasitoids did not readily transfer to cereal aphid pests later.

SHELTER AND MICROCLIMATE

Food and hosts are not the only resources necessary to maintain natural enemy populations. Shelter, particularly during winter, has also been recognised as an important factor governing natural enemy survival and recolonisation rates (van Emden 1990; Thomas *et al.* 1991, 1992a,b; Corbett & Rosenheim 1996; Dyer & Landis 1996; Gurr *et al.* 1998; Wratten et al. 1998). For example, rubidium labeling of a parasitoid of the grape leafhopper *Erythroneura elegantula* (Homoptera: Cicadellidae) in California revealed that non-crop plants (French prune trees) adjacent to vineyards enhanced post-winter recolonisation by the parasitoid (*Anagrus*) in two ways. First, the prune trees harboured an overwintering host of *Anagrus,* which maintained high local parasitoid population densities. Second, the trees also produced a wind-break effect, which increased rates of retention of *Anagrus* from the windstream, immediately downwind of refuges (Corbett & Rosenheim 1996).

Refuges may act simply as shelters from winter temperatures, allowing predators and parasitoids to survive close to or in exposed, harvested fields (e.g., beetle banks; Thomas *et al.* 1991, 1992a,b; Wratten 1992), where they will be required the following year (van Emden 1990; Dyer & Landis 1996; Kidd & Jervis 1996; Gurr *et al.* 1998). Furthermore, when pesticide application is unavoidable, refuges outside the treatment area can be important for natural enemy survival (Kidd & Jervis 1996).

Habitat fragmentation must also be considered, as isolated crop areas may allow pest colonisation and survival in the absence of natural enemies. Kruess and Tscharntke (1994) established islands of red clover to test the effects of habitat connectivity on extinction at different trophic levels. The clover islands were colonised by most available herbivore species, but island isolation reduced parasitoid diversity and rates of herbivore parasitism. In this work, the lack of habitat connectivity released herbivores from parasitism. Isolated, ephemeral habitats are more likely to be colonised by insect species

with good dispersal and colonisation abilities (which is the case for most pest species) rather than natural enemies that require a threshold density of host/prey species before they can begin to establish a population. Isolated fragments can therefore provide, at least temporarily, enemy free space (Jeffries & Lawton 1984) for herbivores.

SYNTHESIS

It is apparent that the theory and practice of biological control may benefit considerably by drawing on ecological theory and that theoretical models may be greatly refined by empirical biological control data.

Guild theory has previously been used to describe interactions between insect natural enemies (Miller & Ehler 1990; Ehler 1992; Godfray 1994) and provides an important theoretical foundation for multiple biological control introductions. The extensive literature on intraguild predation should be examined so that predictions can be made regarding the probability of hyperparasitism within parasitoid guilds. A deeper understanding of these interactions may facilitate the establishment of a natural enemy guild that operates synergistically, rather than competitively. Can a generalist predator, when already present, take over the biological control role of a specialist parasitoid or pathogen following a decrease in pest populations brought about by the specialist agents? Specific knowledge of the population dynamics and feeding range of each organism involved would be necessary for such multi-guild interactions to be exploited, but this knowledge is likely to provide a powerful tool for biological control.

The combination of concepts such as resource subsidies and life-history omnivory can inform, in ecological terms, the enhancement of natural enemy efficacy via the provision of flowers and refuges, two practices that have attracted increasing research effort recently (Thomas *et al.* 1992a,b; Gurr *et al.* 1998; Stephens *et al.* 1998; Wratten et al., 1998; Gurr, Wratten *et al.* 2000; Landis *et al.* 2000). An integration of these subjects has been largely absent and will aid progress in both disciplines. It is not enough to merely observe effects of resource subsidies in the field and attempt to recreate them. Controlled field experiments must be conducted and supported by analyses of the mechanisms operating in specific situations. The next step is to determine the size, shape, and location

of added resources that will provide all the necessary subsidies with a minimum land area taken out of production. Field experiments based on general theory relating to minimum habitat requirements for species conservation (e.g., Doncaster *et al.* 1996) will be important in the determination of resource subsidy requirements. This knowledge could lead to the development of a prescriptive formula to help maximise natural enemy success and provide growers with a viable alternative to pesticides. The spatial scale over which these ecological subsidies have an effect is crucial in terms of applying these concepts in crop-systems management (Gurr, Wratten *et al.* 2000; Landis *et al.* 2000).

Future research in biological control can integrate the appropriate concepts in ecology and agriculture to produce an outcome that is both intellectually and economically rewarding. Adopting ecological theory and using it widely, in an informed way, may hold the key to sustainable agriculture.

Table 2.1: Definitions of several ecological terms and equivalent agricultural terms (where applicable)

Ecological Term	Reference	Concept	Agricultural Term	Reference
Donor control, bottom-up control.	Pimm 1982; Hawkins 1992; Polis 1994; Polis & Strong 1996.	Plants regulate prey populations, which regulate size of predator populations.	Bottom-up control.	Landis *et al*. 2000.
Ecotone/Edge.	Kent *et al.* 1997.	Boundary in spatial landscape mosaic.	Field boundary.	____
Exploitation efficiency.	Chapman & Reiss 1992.	Percentage of the production of one trophic level that is ingested by the trophic level above it.	Loss of yield or degree of pest suppression	____
Food web	Pimm 1980, 1982; Polis 1994; Winemiller & Polis 1996.	Network of consumer-resource interactions among a group of organisms.	____	____
Guild, trophospecies.	Pimm, Lawton & Cohen 1991; Winemiller & Polis 1996.	Sets of organisms with similar prey and predator species.	Natural enemy complex.	____
Intraguild predation.	Polis & Strong 1996.	Feeding on trophically similar consumers.	Hyperparasitism.	Sullivan 1987; Sullivan & Völkl 1999.
Life-history omnivory.	Polis 1994; Polis & Strong 1996.	Shift in diet during development, often accompanied by changes in habitat.	Adult food for parasitoids.	Rabb *et al.* 1976; Landis et al., 2000.
Metapopulation	Taylor 1991.	A collection of spatial population units within which most interaction occurs.	____	____
Multichannel omnivory.	Polis & Strong 1996.	Feeding at different trophic levels, i.e. use of spatial subsidies.	Non-host food / alternative host.	Landis *et al*. 2000.
Non- and quasi- trophic processes, higher order interactions.	Billick & Case 1994; Kareiva 1994; Polis & Strong 1996.	Interactions that do not involve energy transfer.	Behavioural modifications	____
Recipient control, top-down control.	Hawkins 1992; Polis & Holt 1992; Polis & Strong 1996.	Predator populations regulate size of prey populations.	Top-down control.	Landis *et al*. 2000.
Secondary consumer/predator	Chapman & Reiss 1992.	Organism that usually feeds on herbivores.	Natural enemy, beneficial insect, control agent.	____
Spatial subsidy.	Polis & Strong 1996.	Predators/parasitoids receive energy, prey, shelter or detritus from a different habitat, or consumers move among habitats. Equivalent to 'resource subsidy'.	Supplementary resource, companion plant, overwintering site, strip-insectary intercropping, beetle bank.	Rabb *et al*. 1976; Grossman & Quarles 1993; Patt *et al.* 1997b, Landis *et al*. 2000.
Trophic linkage effect, apparent competition, indirect effect.	Strauss 1991; Winemiller & Polis 1996; Janssen *et al.* 1998.	Species A affects C via a direct effect on B.	____	____

CHAPTER 3: MECHANISMS OF ENHANCEMENT OF PARASITOID EFFICACY BY FLORAL RESOURCE SUBSIDIES

INTRODUCTION

There are two mechanisms by which floral resource subsidies can enhance biological control by natural enemies. First, elements of the floral resource may enhance one or more measures of natural enemy fitness, such as longevity or fecundity. In this case per capita attack rates increase, indirectly increasing reproductive output, but natural enemy density is not affected directly. Increases in parasitoid longevity and fecundity as a result of floral resource subsidies are the focus of this chapter.

Second, natural enemies may be attracted to, and aggregate around floral patches (e.g., van Emden 1969; Bowie *et al.* 1999), demonstrating increased effectiveness by virtue of their density, rather than increased per capita efficacy (Chapter 4).

Parasitoid fitness is affected by a suite of environmental variables, several of which can be manipulated using resource subsidies (e.g., Pickett & Bugg 1998, Gurr & Wratten 1999, 2000a; Landis *et al*. 2000). For example, abiotic factors including temperature (Singh, Pandey *et al.* 2000), photoperiod (Sagarra *et al.* 2000) and season (Ellers *et al.* 2001), as well as biotic factors including feeding (Singh, Singh *et al.* 2000, Wäckers 2001) and mating (Starý 1970) can potentially affect parasitoid fitness. The body size (instar) of the host does not appear to affect fecundity or longevity in the F_1 generation of aphidiid parasitoids (Hymenoptera: Aphidiidae), unless daily rates of parasitism are experimentally controlled (Cloutier *et al.* 1981). Rather, when choosing a host, females appear maximise the number of progeny per unit search time (rather than individual offspring quality) by selecting smaller hosts that require less time to attack and subdue (Chau & Mackauer 2001).

A number of studies have demonstrated that sugar can enhance parasitoid longevity (e.g., Dyer & Landis 1996, Heimpel *et al*. 1997; Jacob & Evans 2000; Johanowicz & Mitchell 2000; Sagarra *et al*. 2001) and maximum levels of egg maturation (e.g., Jervis *et al.* 1993, Wheeler 1996). Within the Aphidiidae, experimental provision of carbohydrate-rich bee (*Apis mellifera* L.) honey or aphid (Homoptera: Aphididae) honeydew resulted in a

50% - 480% increase in longevity in *Aphidius smithi* Sharma & Subba Rao (Wiackowski 1961 cited in Starý 1970) and 40% - 210% in *Aphidius avenae* Haliday (Arthur 1944). However, whether floral nectar provides a useful source of carbohydrates for aphidiids in nature remains uncertain (Starý 1970). Other families of hymenopteran parasitoids that feed on floral nectar, such as Braconidae, exhibit gross prolongation of the genae and labio-maxillar complex, that is not apparent in the Aphidiidae. Starý (1970) infers that the absence of these morphological adaptations implies aphidiids do not feed at flowers in nature. However, Jervis *et al*. (1993) observed the aphidiid *Trioxys* sp. probing the corolla opening of *Crepis* sp. (Asteraceae) flowers with its mouthparts. Arthur (1944) found floral nectar feeding to be rare in *A. avenae*, and partially dependent on plant family. Families such as Leguminosae were most attractive and Compositae proved least so. Starved *A. avenae* have been observed to chew holes in the corollae of red clover *Trifolium pratense* L. (Leguminosae) flowers, which would otherwise be too deep for feeding and require larger insects to trip the flower (Arthur 1944). However, this may have been an artefact of laboratory conditions (Starý 1970).

Nectar is not the only potentially useful resource provided by flowers, as pollen is occasionally fed on by hymenopteran parasitoids (Jervis *et al.* 1993). Starý (1964) observed that pollen feeding enhanced longevity in *Aphidius megourae* Starý, although not as markedly as did honey. However, pollen used in this experiment was taken from honeycomb, so honey residue may have been responsible for the increases. It is possible that pollen will not constitute an important resource subsidy, because adult *Aphidius* spp. do not appear to feed on pollen in nature (Starý 1970).

The effect of resource subsidies on parasitoid fecundity is not as clear as their effect on longevity. Flanders (1950) divided hymenopteran parasitoids into two groups based on the proportion of eggs females have matured before the onset of oviposition. Species with the majority of their eggs mature prior to the commencement of oviposition are termed ‘pro-ovigenic’. Pro-ovigenic species have the capacity for a full complement of eggs in the ovaries or oviducts, built from food reserves obtained during the larval stage. Although pro-ovigenic species feed during adult life, these resources are used only for somatic maintenance and to promote longevity (Jervis *et al.* 1993). Conversely, ‘synovigenic’

species do not emerge with a full complement of eggs and continue to mature (i.e., fully chorionate) eggs throughout their reproductive life (for a review of costs and benefits associated with ovigeny strategies, see Jervis *et al.* 2001). Starý (1970) suggested that the Aphidiidae represent an intermediate group between the two ovigeny strategies proposed by Flanders (1950). His evidence was derived from observations that maximum lifetime reproductive success is determined before emergence and ovisorption seldom, if ever, occurs, yet many aphidiids also mature eggs between bouts of oviposition (Starý 1970). However, Flanders' (1950) classification relates to egg maturation, so that maximum potential fecundity (i.e., the number of immature stem line oocytes or oogonia) may be fixed at emergence in synovigenic species. Moreover, ovisorption may also occur in the Aphidiidae (Sedlag 1964, cited in Starý 1970), allowing aphidiids simply to be classified as synovigenic. Further evidence for an intermediate ovigeny status for aphidiids included an observation that *Diaeretiella rapae* McIntosh emerging from overwintering mummies lays only the supply of eggs matured before emergence (Broussal 1961, cited by Starý 1970). However, this may be due to depletion of somatic reserves over winter and an absence of floral resource subsidies early in the season. Starý (1970) doubted the importance of adult food for egg maturation, but conceded that its role in aphidiid fecundity requires further research (e.g., Völkl 1994b; Singh et al. 2000).

This chapter examines the effects of floral resource subsidies on parasitoid longevity and egg production, two life-history parameters that can greatly limit lifetime reproductive success (Rosenheim 1996; Heimpel *et al.* 1998; Sevenster *et al*. 1998; Rosenheim 1999; Rosenheim *et al*. 2000).

Theoretical models have attempted to predict whether parasitoids are primarily egg- or time-limited; that is, whether lifetime reproductive success is dependent on available time for host searching and oviposition, or available physiological resources for egg maturation (Heimpel *et al.* 1996; Rosenheim 1996; Heimpel *et al.* 1998; Sevenster *et al.* 1998; Rosenheim 1999; Rosenheim *et al.* 2000). Furthermore, every oviposition event carries a certain opportunity cost, such that time or eggs used on a given host become unavailable to search for or oviposit on a potentially "higher quality" host (Rosenheim 1996), if host quality rather than number of progeny is being maximised.

Early models (e.g., Rosenheim 1996) focused on pro-ovigenic species, in which the total resources available for egg production are fixed at eclosion. Assuming an optimal egg size, Rosenheim (1996) predicted that the proportion of parasitoids becoming egg limited will be the proportion that live to reach age $R/$sk days, where R is the amount of resources available for reproduction, s is egg size (so that total potential fecundity is R/s) and k is the host encounter rate per day. However, in synovigenic species, R can be adjusted according to the physiological state of the female. Resources can be mobilised from other functions to mature eggs (Rivero & Casas 1999a), or conversely, mature eggs can be resorbed (Rosenheim *et al.* 2000) as required. A recent model of egg limitation in synovigenic species shows that the most important constraint on fitness is the rate of egg maturation (Rosenheim *et al.* 2000).

The present study examines whether, and to what extent, certain elements of floral resources enhance parasitoid survival and reproduction. Two resource elements, sugar and buckwheat *Fagopyrum esculentum* Moench pollen, are provided to parasitoids and their effects on longevity and egg load (through time) are experimentally tested.

The experiments involve two species of synovigenic aphid parasitoid (Hymenoptera: Aphidiidae), *Aphidius rhopalosiphi* DeStefani-Perez and *Diaeretiella rapae*. *A. rhopalosiphi* was used because it was the most common naturally occurring species in experimental wheat fields (Chapter 4). *Diaeretiella rapae* was selected to test whether any effects of resource subsidies on *A. rhopalosiphi* were species-specific, or represent a general pattern among members of the Aphidiidae.

METHODS

General Methods

Two experiments were conducted on each of the above two species of parasitoid to determine the effects of floral resource subsidies on longevity and egg load. Experimental treatments were established in a 15^{o}C controlled temperature room, with a reversed 12 hr day/night cycle, at the University of Canterbury, Christchurch, New Zealand.

Mummified (parasitised) aphids were placed individually in 75 ml plastic Labserv™ containers with a damp piece of tissue paper. Each container had a circular hole (6 mm diameter) in the lid with a 500 μm mesh covering. Individual parasitoids were randomly allocated to one of several treatments to assess the effects of resource provision on longevity or egg load. The treatments included pollen, nectar, and in one experiment, a male for mating. A gel mixture containing 0.25g agar, 5g honey, 5g sucrose and 25 ml distilled water was used as a substitute for nectar so that parasitoids would not become trapped and drown in a solution of sugar. Pollen was cut from the stamens of one buckwheat *Fagopyrum esculentum* c.v. 'Kitawase' plant. Each parasitoid in the pollen treatment received a quantity of pollen equivalent to that provided by five buckwheat flowers.

All statistical analyses were conducted using MINITAB™ version 13.1. Before parametric tests were performed, the data were tested for normality using the Ryan-Joiner normality test, which is a correlation-based analysis similar to the Shapiro-Wilk test, and the Kolmogorov-Smirnov test, which is an ECDF (empirical cumulative distribution function) based test. As there was no discrepancy in the conclusions drawn by the two tests, only results from the Ryan-Joiner test are presented, as these yield both R- and P-values, whereas the Kolmogorov-Smirnov test yields only P-values.

Longevity experiments

Parasitoid emergence and death were recorded at 12-hour intervals to assess the effects of resource subsidies on parasitoid longevity.

Aphidius rhopalosiphi

Experiments on *A. rhopalosiphi* were carried out from 29 November 2001 to 10 January 2002. Mummies used in this experiment were collected from the Biological Husbandry Unit at Lincoln University during field surveys (see Chapter 4), and randomly assigned to different treatments. At this point in time the species of parasitoid within the mummies was unknown. Approximately 100 mummies were collected and exposed to treatments, but only 45 females were used in the final analysis, as the absence of a

published key for male Aphidiidae made reliable identification impossible. Parasitoid and hyperparasitoid species other than *A. rhopalosiphi* were too rare to allow statistical analysis, so data for these species were discarded.

Fifteen individual *A. rhopalosiphi* females were provided with sugar gel, 15 individuals were provided with buckwheat pollen, and 15 individuals in the control treatment were given no resource provisioning (only damp tissue paper, as in all other treatments). Comparisons of longevity between treatments were made using one-way analysis of variance (ANOVA) on untransformed data. Post-hoc comparisons of means were conducted using Tukey's pairwise comparisons.

Diaeretiella rapae

Mummified aphids containing *D. rapae* were obtained from Bioforce Ltd. (Auckland, New Zealand). As individuals of this species were obtained from a culture (and sample sizes were limited), males and females were assumed to be of the same species, so no distinction was made between sexes for the purposes of analysis. This experiment was conducted from 16 April to 5 May 2001

Twenty parasitoids were individually exposed to sugar gel and 20 were only provided with only damp tissue paper (controls). No pollen treatment was used in this experiment. Comparisons of longevity between treatments were made using a two-sample t-test of $\log_{10}$-transformed data.

Egg load experiments

A series of laboratory experiments was conducted to determine the effects of resource subsidies on parasitoid egg load.

Aphidius rhopalosiphi

Female *A. rhopalosiphi* used in this experiment were collected from the Biological Husbandry Unit (see above) and maintained in culture at Lincoln University. The experiments were carried out between 6 February and 25 March 2002. Twenty-five newly-

emerged female parasitoids were individually assigned to each of three treatments to examine the effects of floral resources on egg load. The treatments comprised sugar gel, buckwheat pollen and a control (damp tissue paper) treatment. Five randomly selected females from each treatment were euthanised and dissected at each of five time intervals (6, 12, 24, 48 and 72h) to assess egg load. Ovaries were removed by grasping the ovipositor with fine forceps and gently pulling until the ovipositor and ovaries became detached from the abdomen. Ovaries were placed on a slide and stained with a 0.01% solution of methylene blue. Pressing gently on the cover slip caused the ovaries to burst, releasing the eggs which could then be counted under a dissecting microscope. Only fully matured eggs were recorded, because egg maturation may vary, whereas the number of oogonia (immature eggs) is fixed at eclosion.

Data were analysed using a two-way ANOVA on untransformed data, with time and treatment as fixed variables. Subsequently, one-way analyses of variance were conducted to make post-hoc comparisons between treatments at each time interval.

Diaeretiella rapae

Female *D. rapae* were obtained from Bioforce Ltd and experiments were conducted between 8 July and 23 August 2001. Twenty-five newly-emerged female parasitoids were individually assigned to each of four treatments, three of which were identical to those of *A. rhopalosiphi,* with a further treatment consisting of a male parasitoid available for mating. As with *A. rhopalosiphi,* five randomly selected females from each treatment were dissected at each time interval and egg load was measured.

Data for *D. rapae* were analysed in the same way as those for *A. rhopalosiphi*.

RESULTS

Longevity experiment

Aphidius rhopalosiphi

Survival times of *A. rhopalosiphi* females ranged from 1.5 – 7.0 days in controls, 2.0 – 6.5 days in females provided with pollen and 6.0 – 15.5 days in females provided with sugar. Data for the three treatments (control, sugar and pollen) were all normally distributed

(Ryan-Joiner test: R > 0.97, P > 0.1 in all cases). Parasitoids exposed to the sugar treatment survived, on average, between three and four times as long as those in the control or pollen treatments (Fig 3.1a). Longevity was significantly different between treatments (one-way ANOVA: $F_{(2, 42)} = 54.23$, $P < 0.001$). Females in the sugar treatment survived significantly longer than those in control or pollen treatments. However, longevity of females in the pollen treatment did not differ significantly from that of females in control treatments (Tukey's pairwise comparisons).

Diaeretiella rapae

Longevity of *D. rapae* ranged from 2.0 – 6.5 days in control individuals and 2.5 – 14.0 days in those provided with sugar. The data were $\log_{10}$ transformed to achieve normality (Ryan-Joiner test on $\log_{10}$ transformed variates: R > 0.97, P > 0.1 in both cases). Longevity was significantly greater in individuals provided with sugar than in control individuals (t-test: t = - 4.0, P < 0.001, d.f. = 38; fig 3.1b).

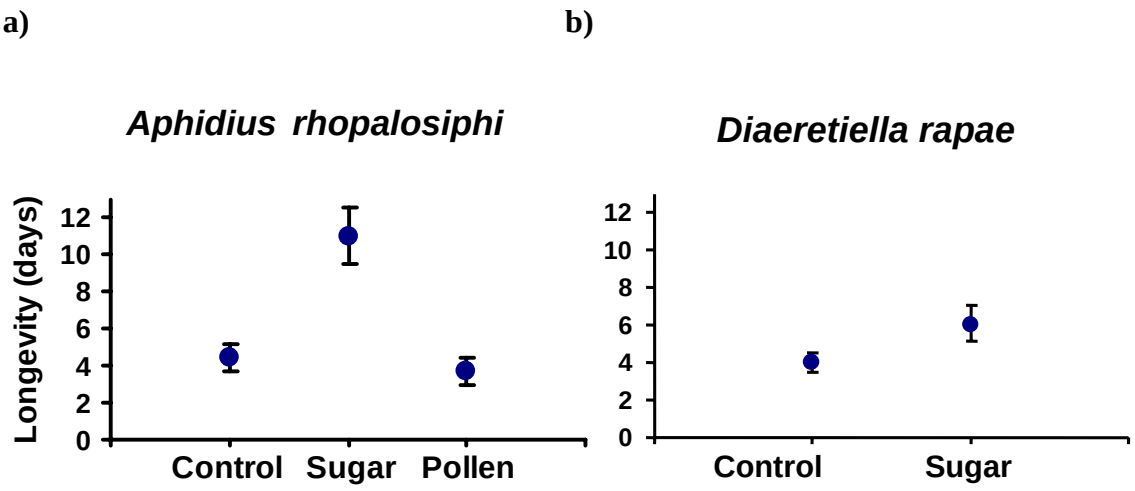


Figure 3.1: Mean (+/- 95% C.L.) longevity of a) *Aphidius rhopalosiphi* and b) *Diaeretiella rapae* in control (damp tissue only), sugar gel and pollen (*A. rhopalosiphi* only) treatments. Mean and confidence limits for *D. rapae* are back-transformed from $\log_{10}$-transformed variates.

Egg load experiment

Aphidius rhopalosiphi

Egg load ranged from 23 to 145 across all treatments and time intervals. Mean egg load varied significantly with treatment ($F_{(2, 60)} = 14.3$, $P < 0.001$) and time ($F_{(4, 60)} = 36.49$, $P < 0.001$), but not all treatments had the same effect on egg load through time (treatment x time interaction effect, $F_{(8, 60)} = 6.59$, $P < 0.001$) (Fig. 3.2a).

Provision of sugar significantly increased egg load over control and pollen treatments at 48 h (one-way ANOVA: $F_{(2, 12)} = 5.25$, $P = 0.023$) and at 72 h ($F_{(2, 12)} = 17.24$, $P < 0.001$), but not at earlier time intervals (6, 12 and 24 h, all $p > 0.005$) (Fig. 3.2a).

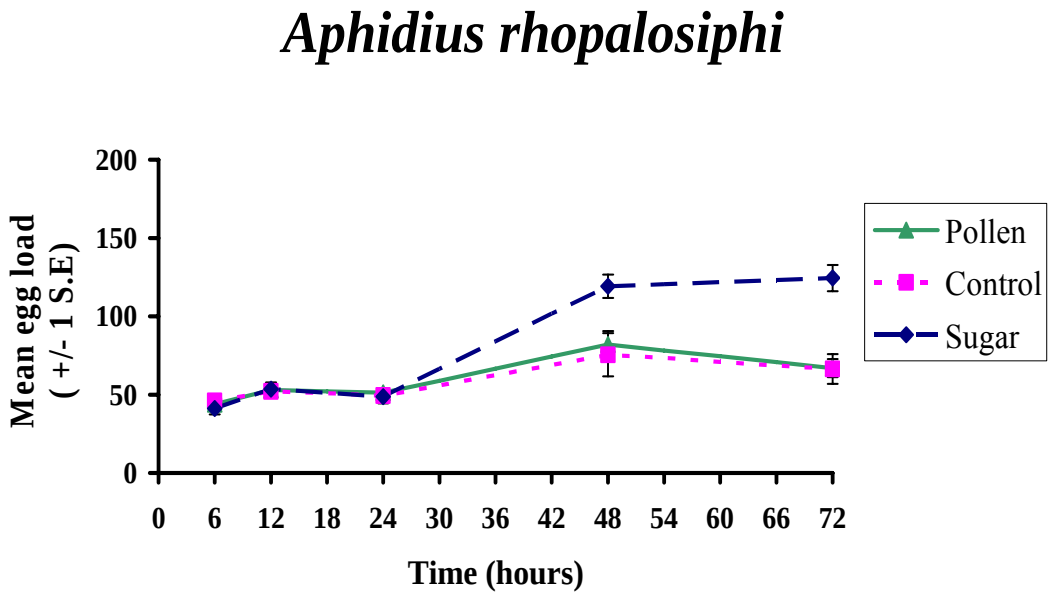
Diaeretiella rapae

Egg load ranged from four to 207 across all treatments and time intervals. As with *A. rhopalosiphi*, *m*ean egg load of *D. rapae* was significantly affected by treatment ($F_{(3, 80)} = 15.89$, $P < 0.001$) and time ($F_{(4, 80)} = 3.85$, $P = 0.007$), and the variation in egg load with time was not the same for every treatment (treatment x time interaction effect, $F_{(12, 80)} = 4.37$, $P < 0.001$) (Fig. 3.2b). Provision of sugar significantly increased egg load over control and pollen treatments at 48 h (one-way ANOVA: $F_{(3, 16)} = 7.63$, $P = 0.002$) and at 72 h $F_{(3, 16)} = 21.73$, $P < 0.001$). As with *A. rhopalosiphi*, there was no significant effect of treatment on egg load at the earlier time intervals (6, 12 and 24 h, all $p > 0.005$) (Fig. 3.2b).

DISCUSSION

Resource subsidies increase the resource 'capital' that a parasitoid has available for allocation to one or more life-history parameters (Rivero & Casas 1999a). Both *Aphidius rhopalosiphi* and *Diaeretiella rapae* were able to use these resources to mature eggs and increase their longevity, thus increasing their potential fecundity. This effect of sugar on egg load was also observed when honeydew was provided to the aphidiid *Lipolexis scutellaris* Mackauer (Singh *et al*. 2000). This contrasts with the suggestion by Starý (1970) that adult food is unimportant for egg maturation in aphidiids, and confirms the synovigenic status of the Aphidiidae. Furthermore, the increase in egg load exhibited by

a)


Aphidius rhopalosiphi
Mean egg load
(+/- 1 S.E)
200
150
100
50
0
0 6 12 18 24 30 36 42 48 54 60 66 72
Time (hours)
Pollen
Control
Sugar

b)

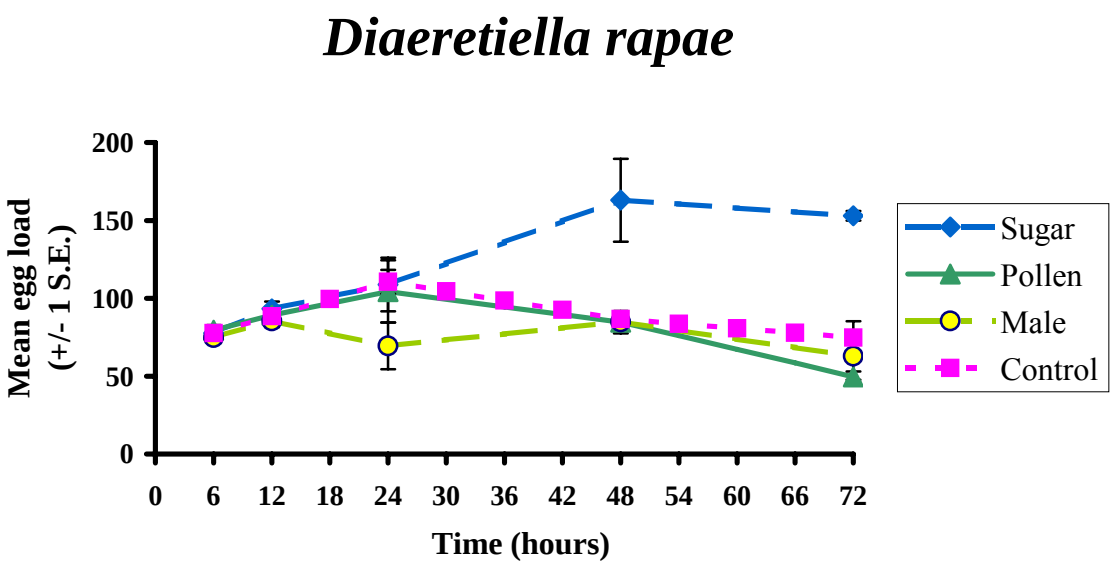

Diaeretiella rapae
Mean egg load
(+/- 1 S.E.)
200
150
100
50
0
0 6 12 18 24 30 36 42 48 54 60 66 72
Time (hours)
Sugar
Pollen
Male
Control

Figure 3.2: Egg load (measured by dissection) of a) *Aphidius rhopalosiphi* and b) *Diaeretiella rapae* at 6, 12, 24, 48 and 72 hours post-emergence, in control (damp tissue only), sugar gel, pollen and male for mating (*D. rapae* only) treatments.

females in the sugar treatments may be conservative if the maximum egg load recorded (145 eggs in *A. rhopalosiphi,* and 207 eggs in *D.* rapae) represents a limit on the capacity for egg storage in these species. If oviposition were occurring, more eggs might be able to mature, increasing maximum potential fecundity. This scenario becomes especially plausible if nutritional resources can be used for egg maturation over a long period of time, as demonstrated by Rivero & Casas (1999b), and concomitantly to increase longevity.

It seems logical that if resource subsidies allow an increase in egg load, time is likely to become a limiting factor. Time is considered to be limiting if a parasitoid dies without exhausting its supply of mature eggs (Heimpel *et al.* 1998; Sevenster *et al.* 1998; Rosenheim 1999), i.e., before age *R/sk*. The proportion of parasitoids becoming time limited can be approximated to $1 - e^{-\mu R/sk}$ (adapted from Rosenheim 1996), where μ is the constant daily mortality rate. Both *A. rhopalosiphi* and *D. rapae* showed significant increases in longevity when provided with sugar gel. However, this increase in longevity will only marginally reduce the likelihood of time limitation if mortality rate, μ, is determined by, for example, high predation pressure rather than physiological factors.

Resource subsidies can therefore significantly enhance both longevity and fecundity in the two species of Aphidiidae examined. To what extent the females trade off one parameter over the other is uncertain. Egg resorption can potentially reverse the flow of nutrients from the soma to the oocytes, allowing a form of bet hedging in nutrient allocation. However, this flexibility in resource allocation serves to increase the range of conditions under which egg limitation can occur, as egg costs in synovigenic species may predominate when hosts are either abundant or rare (Rosenheim *et al.* 2000). Evidence for oosorption in this study came from the control and pollen treatments of *D. rapae*, where egg load showed a slight decline after 24 hours. Sample sizes were small; however, so strong conclusions regarding oosorption in the Aphidiidae cannot be made from the

available data. Starý (1970) suggests that oosorption is rare or absent within the Aphidiidae, but cites evidence by Sedlag (1964) showing a decline in egg load with time, similar to that observed for *D. rapae* in the present study. The presence or absence of ovisorption in aphidiids therefore warrants further investigation.

The relative importance of egg- versus time-limitation is greatest in an evolutionary context. At spatial and temporal scales relevant to ecological interactions, individual parasitoids will probably fall somewhere along a continuum between extremes of egg and time limitation (Rosenheim 1999). The interplay of multiple selective forces in the environment (e.g., predation risk and/or environmental adversity) may force individuals to incur opportunity costs from suboptimal search or oviposition decisions without actually becoming egg or time limited (Rosenheim 1999).

The plasticity of longevity and egg load exhibited by *A. rhopalosiphi* and *D. rapae* bears evolutionary significance, but the individual fitness benefit of a parasitoid receiving resource subsidies is probably not evolutionarily relevant. Despite this, it is short term individual- and population-level responses that are of primary importance in biological control. If individual biological control agents exhibit a 50 – 100% increase in egg load and a 50 - 400% increase in longevity in response to floral resource subsidies (as was exhibited by parasitoids in this study), population-level attack rates should show dramatic improvement. Although individual floral resources are too unpredictable to exert significant selection pressures, the mechanisms established in this study show that resource subsidies have the potential to greatly enhance aphid parasitoid fitness on a time scale pertinent to biological control.

Sugar gel was the only resource examined that significantly affected parasitoid fitness. Precisely which element of the mixture (agar, honey or sucrose) enhanced the parasitoids is unclear. Sugar and honey increase longevity in aphidiid (Arthur 1944; Wiackowski 1961 referred to in Starý 1970; Starý 1964) and non-aphidiid (Dyer & Landis 1996; Jacob & Evans 2000; Johanowicz & Mitchell 2000; Irvin *et al*. in press) parasitoids. Similarly, carbohydrates increased longevity in *Aphytis* spp., (Hymenoptera: Chalcidoidea: Aphelinidae) but were insufficient for egg maturation (Rosenheim *et al.* 2000). Aphid honeydew mixed with honey also increased fecundity in the aphidiid *Lipolexis scutellaris*

(Singh *et al.* 2000). Aphid honeydew and nectar contain amino acids and vitamins as well as sugars (Baker & Baker 1973; van Lenteren *et al.* 1987). Agar, contained in the sugar gel used in these experiments, may provide similar nutrients. Egg production requires protein that must be derived either from somatic reserves obtained during the larval stage, or from food ingested as an adult. In species that can mature eggs on a carbohydrate-only diet, the former mechanism (i.e., use of somatic reserves) must operate.

Honeydew is potentially a very valuable resource for aphid parasitoids (Singh *et al.* 2000). However, to reduce peak aphid densities (and economic damage) high early season rates of parasitism are necessary (Settle *et al.* 1996; Wratten *et al.* 1998). If high densities of aphids are required before the nutritional needs of a parasitoid population can be met, it may be too late for the purposes of biological control and another source of sugar (e.g., floral nectar) must be sought.

Pollen appears to be of no direct importance to aphidiids, as no increase in fecundity or egg load was recorded in pollen treatments. This contrasts with the increase in longevity observed in pollen-feeding *Aphidius megourae* (Starý 1964), but as noted above, the increase reported by Starý (1964) may have been due to the honeycomb from which the pollen was gathered. The only parasitoids that show mouthpart specialisations for pollen feeding are Mutillidae and Scoliidae (Jervis 1998). Consumption of pollen by species outside these taxa is more likely to be inadvertent (e.g., while feeding on nectar) than deliberate (Jervis 1998).

The effect of mating on longevity was not examined in this study. The observations of Broussal (1966 referred to in Starý 1970) that longevity was greater in mated females contrasts with other studies (e.g., Jacob & Evans 2000) that demonstrate a longevity cost to mating. The longevity costs and benefits of mating in Aphidiidae require further investigation. It is possible that male ejaculates contain nutrients that are available to the female (a phenomenon that is common among insects), thus providing a form of resource subsidy.

Mating has been shown to positively affect fecundity and longevity in *D. rapae* (Broussal 1966 cited in Starý 1970). No such effect was observed in the present study, with mean egg loads for mated females not significantly different from those of unmated control

females. Aphidiidae are haplodiploid, with unfertilised eggs becoming male and fertilised eggs becoming female. If there were a fitness advantage to producing female offspring, which is plausible given that sex ratios are often female-biased in aphidiids (reviewed in Starý 1970), mated females should invest more resources into egg production, and less into mate location, while unmated females should invest as much as possible into mate location. This effect was not observed in the present study, perhaps because the act of mating itself is energetically expensive. In addition, there may be significant resource competition between males and females such that there is a resource cost to mating that would need to be outweighed by the fitness benefits of producing female offspring.

In summary, carbohydrate-rich resource subsidies can enhance efficacy of aphidiid parasitoids via increases in longevity and egg load. Such increases in potential fecundity provide a mechanistic explanation for the increased rates of parasitism observed when floral resources are available to certain species of parasitoid (e.g., Letourneau, 1987; Chaney et al 1998; Stephens *et al.* 1998). Whether these increases in potential fecundity translate into increased realised fecundity (i.e., reproductive success) requires further investigation. Moreover, the ability of aphidiid parasitoids to obtain these resources from flowers in nature and the spatial scale across which the effects of floral resources can be observed remain unclear. These problems will be addressed in Chapter 4.

CHAPTER 4: ENHANCEMENT OF PARASITOID POPULATIONS USING FLORAL RESOURCE SUBSIDIES: TESTING THE MECHANISMS

INTRODUCTION

Several authors have examined the effects of floral resources on local densities of natural enemies in agricultural systems (e.g., van Emden, 1962; Root 1973; Hickman & Wratten, 1996; Hooks *et al*. 1998; Berndt *et al.* 2002). Floral resources may directly increase natural enemy densities by reducing emigration, while colours and scents of flowers may attract other predators and parasitoids from areas lacking these resources (Haslett 1989). Concomitantly, natural enemies that utilise floral resources exhibit increased longevity and egg load (Chapter 3), which may indirectly increase population densities through increased reproduction. Increased reproduction or immigration, combined with reduced emigration leads to increased local abundance of natural enemies in areas containing floral resource subsidies (van Emden, 1962; Smith, 1969; Horn, 1981; Bugg *et al.*, 1991; Costello & Altieri, 1995; Theunissen *et al.*, 1995; Hickman & Wratten, 1996; Montandon & Slosser, 1996; Lehmhus *et al.*, 1996, 1999; Goller *et al.*, 1997; Vidal, 1997; Stephens *et al.* 1998, but see Root 1973; Costello & Altieri 1995; Moreby & Sotherton 1997; Hooks *et al*. 1998; Berndt *et al.* 2002). However, the extent to which natural enemy fitness is enhanced and the spatial scale over which effects on immigration and emigration operate, remain to be determined (Landis *et al*. 2000). Moreover, in a natural environment, other factors such as aggregated numerical responses to patches of high host density (May 1976; Jarosik & Lapchin 2001), crop edge (Dyer & Landis 1997; Williams & Martinson 2000) or windbreak effects (Corbett & Rosenheim 1996) may overwhelm the effects of floral resource subsidies on natural enemy aggregation.

The aim of this chapter is to determine whether floral resource subsidies enhance realised fecundity (i.e., rates of oviposition) of *A. rhopalosiphi* in the laboratory and field through a combination of increased longevity and egg load (Chapter 3). Laboratory experiments involve the provision of essentially limitless aphids to test maximum fecundity under different resource treatments. Field surveys and experiments are presented that

examine whether floral patches enhance rates of parasitism, and the spatial scale over which any effects operate. Field studies were conducted under controlled and natural aphid densities to determine whether density dependence in rates of parasitism outweighs effects of resource subsidies on parasitoid aggregation. However, density dependence may be difficult to measure, as it can operate differently at different spatial scales. For example, Jarosik & Lapchin (2001) demonstrated that rates of parasitism of *Myzus persicae* Sulzer by *Aphidius colemani* Viereck were density dependent at the scale of whole plants, but inversely density dependent at the shoot and leaf scale.

Other factors that may potentially influence rates of parasitism, such as edge and windbreak effects, are also examined. Edge effects may result from initial colonisation of crop edges by parasitoids and slow subsequent dispersal into the crop interior (Williams & Martinson 2000) or by the use by natural enemies of non-crop plants at the field margins (Dyer & Landis 1997). However, higher parasitoid densities at only one edge may be indicative of windbreak effects on parasitoid colonisation (Corbett & Rosenheim 1996).

METHODS

Microcosm experiments

Laboratory experiments were conducted to determine whether increases in life-history parameters as a result of resource subsidies (as described in Chapter 3 translate into an increase in rates of parasitism. Aphids (*M. dirhodum*) used in these experiments were obtained from Crop and Food Research, Lincoln, New Zealand; female *A. rhopalosiphi* were reared from parasitised aphids collected from the Biological Husbandry Unit (BHU), Lincoln University and both were maintained in culture at Lincoln University, under the conditions described above.

Experiments were carried out in Perspex chambers in one 15^{o} C 16/8h day/night cycle controlled environment room at Lincoln University from 24 February – 14 April 2002. Four treatments were conducted simultaneously in different chambers and repeated four times. Each experimental chamber contained a female parasitoid (*A. rhopalosiphi*), water and a pot of wheat *Triticum aestivum* (L.) (Gramineae) (c.v. Wasp) seedlings containing approximately 300 aphids (*M. dirhodum*). This provided a 'limitless' supply of

potential hosts, so that maximum rates of parasitism could be recorded. The first experimental treatment was a control, with no additional resources provided. Sugar gel (see Chapter 3 p.33 for composition) was provided to females in the second treatment, and the third comprised buckwheat plants with all flowers removed. The final treatment included an entire buckwheat *Fagopyrum esculentum* Moench (Polygonaceae) (c.v. Kitawase) plant to test whether the resources of this species can be utilised by *A. rhopalosiphi*, and whether the combination of several floral resources produces different effects to each of the resources (e.g., pollen and sugar) in isolation.

Each experiment ended with the death of the female parasitoid. When a dead parasitoid could not be found, a parasitoid was assumed to be dead if it had not been observed for three days. If mummified aphids appeared on the wheat seedlings prior to parasitoid death, the pot was replaced with another, containing approximately 300 aphids. This was necessary to prevent new parasitoids emerging during the experiment.

After a period of seven days following removal of a pot or termination of an experiment, aphids were examined for signs of mummification, and the number of aphids parasitised per treatment was recorded.

Comparisons of rates of predation between treatments were made using a one-way ANOVA with post-hoc comparisons of means using a Tukey's pairwise comparison. All statistical analyses were conducted on MINITAB 13.1

Field studies

Study site

All field surveys and experiments were conducted at the BHU, located approximately 1 km Southwest of Lincoln University, Canterbury, New Zealand (Fig. 4.1). The BHU was established in 1976 as a 0.2 ha. experimental organic farm. One field (Fig. 4.1, field 1) used in the present study is located in a 4 ha. paddock that was taken over by the BHU in 1988. The other field (Fig. 4.1, field 2) is located in the Chapman Block, which became part of the BHU in ca. 1980. No synthetic pesticides or herbicides are used at the BHU.

Figure 4.1: Aerial photograph of Biological Husbandry Unit, Lincoln, New Zealand. Fields 1 and 2 marked red.

Field 1 measured approximately 32 m x 150 m and field 2 was approximately 57 m x 130 m. Fields 1 and 2 were drilled with wheat *T. aestivum* (c.v. Otane) on 1 October 2001. A 5 m x 5 m patch of buckwheat *F. esculentum* (c.v. Kitawase) was hand sown 20 m from each end of each field (Fig. 4.2). The four patches were partially sown (approximately 50% cover) on 4 – 5 October 2001, and the remaining 50% of each patch was sown on 26 – 30 November 2001. This produced two cohorts of buckwheat plants, approximately one month apart, so that the second cohort was still flowering after the first had ceased. A 1 m x 1 m patch of wheat was left in the centre of each buckwheat patch to allow measurement of parasitism rates within the patch.

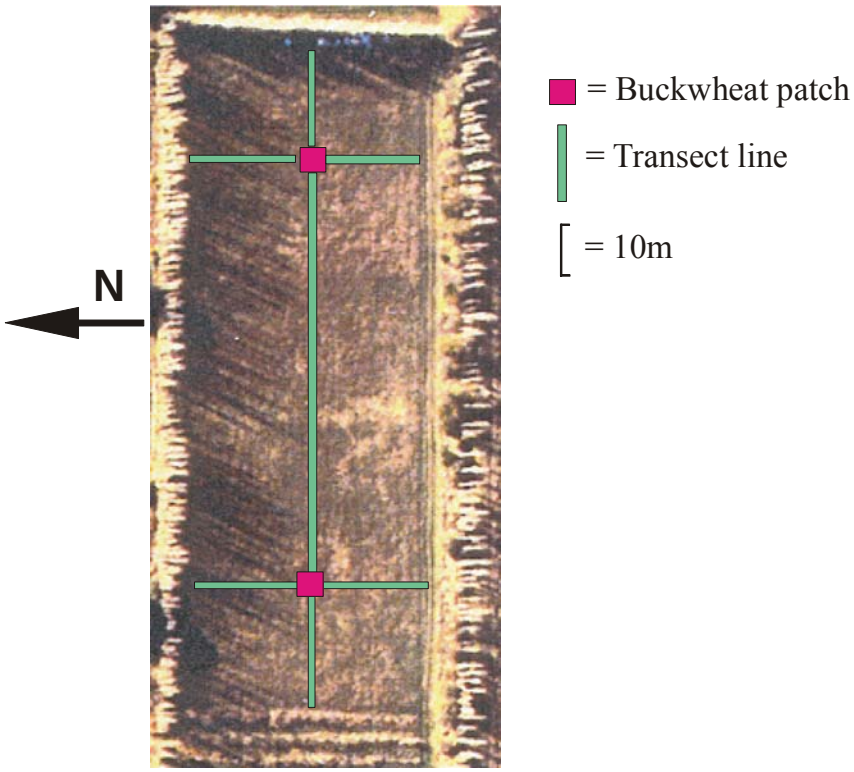


Figure 4.2: Diagram of layout of field 2, showing transect lines and position of buckwheat patches. The central area was planted with wheat *Triticum aestivum*; borders are shelter belts of poplars *Populus* spp. The layout of field 1 was identical.

Four transects radiating from each side of each buckwheat patch were measured and marked with bamboo stakes at 2 m intervals, such that one transect ran between the two

floral patches in each field and a further three transects ran from each patch to the edges of the field (Fig. 4.2). Field surveys and experiments were conducted along these transects.

When distances from buckwheat patches were measured, a 1 m^2 patch of wheat within the buckwheat was considered to be the 0 m point, and the edge of the buckwheat patch was recorded as a 2 m distance from the zero point.

Field surveys

Surveys of live and mummified aphids were conducted to examine the effects of resource subsidies, proximity to field edges and host density on naturally occurring aphid densities and rates of parasitism. Two surveys were conducted in field 1 (7 and 28 December 2001, termed survey 1 and 2 respectively) and four were conducted on field 2 (3, 14 and 26 December 2001 and 3 January 2002, termed survey 3-6 respectively).

Each survey involved removal of three wheat plants every 2 m along the centre transect, and the counting of aphids and mummies present on each plant. In survey 2, radial transects were also surveyed.

Total numbers of aphids and mummies at each 2 m pointwere divided by three to determine the mean number per plant. Non-normally distributed data sets were square-root transformed to achieve normality. Linear regressions were conducted to determine whether numbers of aphids and mummies at each point along the transect were correlated with distances from the leeward end of the field (End), the nearest edge (Edge), or the nearest floral patch (Patch). Linear regressions were also conducted to determine whether numbers of mummies were correlated with aphid density (in either the same or previous surveys) at the same location. Statistical analyses were conducted in MINITAB 13.1 and Statistica 6.0.

Field manipulations

Manipulative field experiments were conducted to determine the effects of floral resource subsidies on rates of parasitism at a fixed aphid density. Experiments began after natural aphid populations had declined to below 0.5 aphids per 100 plants. Two trials were conducted in field 1 (beginning on 4 and 9 January 2002 respectively) and one was conducted in field 2 (beginning on 7 January 2002). After mid-January, wheat plants began

to yellow to an extent that greatly reduced survival of experimental aphids, and experiments ceased.

Experimental aphids were placed in the field using small cages that were clipped onto a leaf, providing shelter while aphids adjusted to the new environment. Clip cages were constructed from 14 mm diameter plastic tubing, cut cross-sectionally to 15 mm lengths. Each section of tubing had a plastic 500 µm mesh covering glued to one end and a ring of 3 mm thick foam rubber glued to the other. A Lady Jane® flat curl hair clip (model 2811) was bent and glued to two sections of tubing to form miniature tongs, based on the methods presented by Noble (1958) (Fig. 4.3).

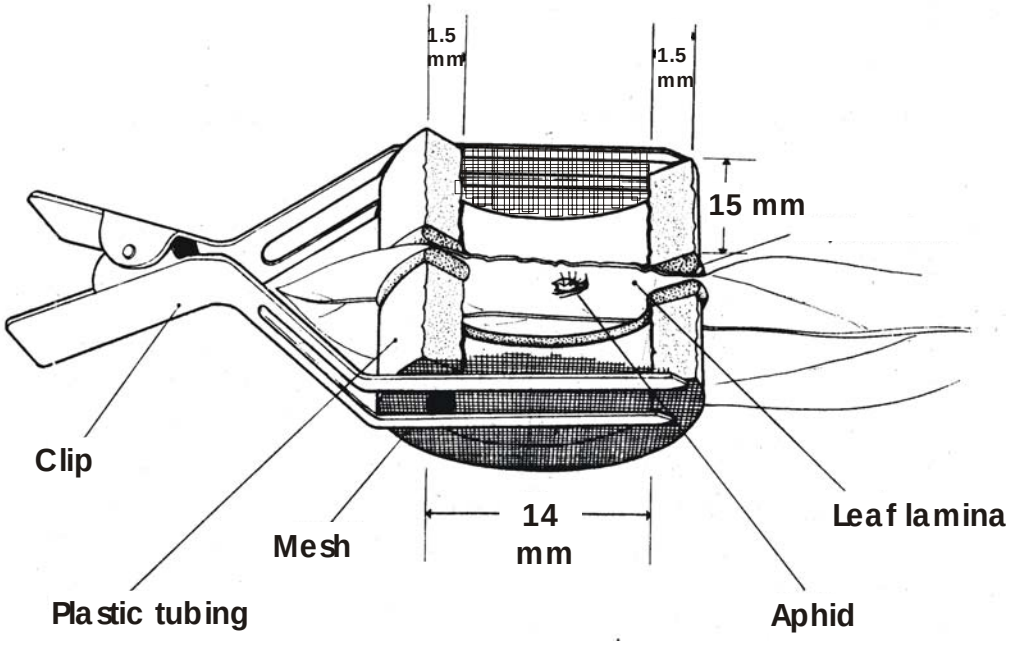


Figure 4.3: Diagram of clip cage (adapted from Adams & van Emden 1972).

Five final-instar wingless aphids (*M. dirhodum*) were clip-caged onto the abaxial surface of highest (flag) leaf of wheat plants positioned at 4 m intervals along each transect. Leaves with clip cages were marked with a 4 mm x 20 mm section of white parcel tape folded around the leaf. Two days after the aphids were positioned, the clip cages were removed to expose aphids to parasitism. Any first-instar aphids produced during this two-day period were removed so that five aphids were exposed to parasitism in each replicate.

After two days of exposure, any aphids that were still present were removed and reared at 15^{o} C for 7 days and the proportion of aphids mummified was recorded.

Logistic regressions were conducted to assess whether rates of parasitism were correlated with distances from floral resource patches, nearest edges or the leeward end of the field. Statistical analyses were conducted on Statistica 5.5 and 6.0.

RESULTS

Microcosm experiments

The number of aphids parasitised out of approximately 300 provided ranged from 82 in a control treatment to 167 in a sugar treatment and was normally distributed among treatments (Ryan-Joiner test: R > 0.94, P = 0.067). There was significant variation in the levels of parasitism among treatments (one-way ANOVA: $F_{(3,12)} = 5.44$, P = 0.014); however a Tukey's pairwise comparison revealed that only the difference between control and sugar treatments was significant (Fig. 4.4).

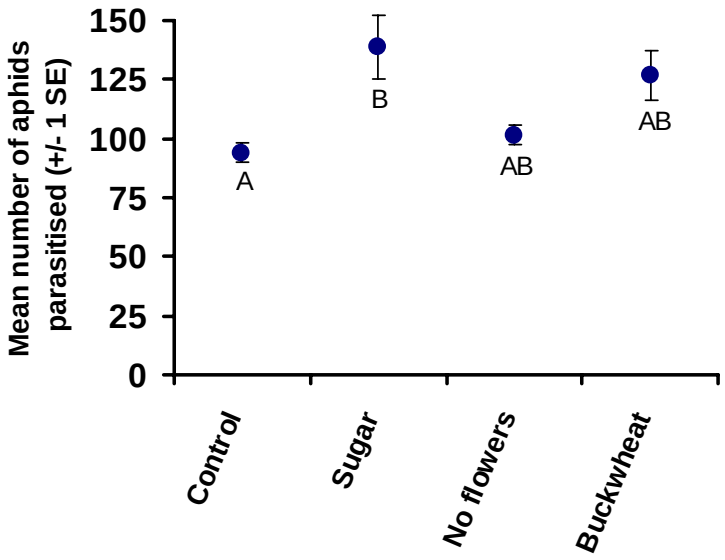


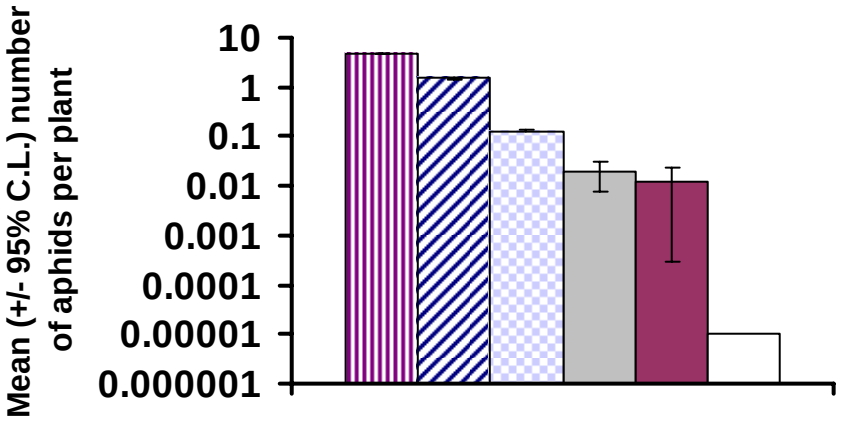
Figure 4.4: Mean (+/- 1 SE) number of *Metopolophium dirhodum* parasitised by *Aphidius rhopalosiphi* in treatments comprising a control (water only), sugar gel, buckwheat plant with flowers removed or whole buckwheat plant. Differences between means (from Tukey's pairwise comparisons) are indicated by A or B below data points. AB indicates no significant difference from A or B.

Field studies

Field surveys

Aphid densities in both fields showed a significant decline through time (linear regression on log (aphid density + 0.00001): $R^2 = 0.84$, $F_{(1,5)} = 21.18$, $P < 0.010$) (Fig. 4.5a). Parasitoid densities showed a different trend, rising to a peak in mid December (survey 4), then decreasing as the season progressed (Fig. 4.5b).

a)



b)

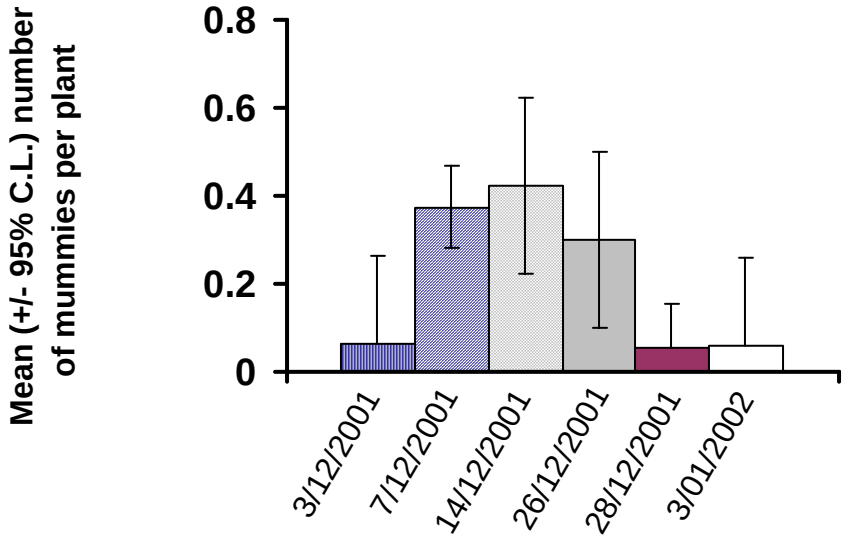


Figure 4.5: Mean (+/- 95% C.L.) number of a) *Metopolophium dirhodum* (+ 0.00001) and b) parasitised *Metopolophium dirhodum* (mummies) per wheat plant in field surveys over time.

Aphid densities were affected by 'End' distance in 3 of the 5 surveys where aphids were present, by 'Edge' distance in 2 out of 5 surveys and by Patch distance in only one survey (Table 4.1). In surveys demonstrating Edge, End and Patch effects on aphids, there were no such effects on levels of parasitism (Fig. 4.6).

Linear regressions revealed very few trends in parasitism levels related to 'Edge' 'End' or "Patch' distances (Table 4.1). Only survey 2 revealed a significant increase in the number of parasitism events per plant (with respect to Edge distance), but the regression equation explained only 9.3% of the variation in the data (Table 4.1).

There was no correlation between levels of parasitism and aphid density at the same transect location in either the same or the previous survey (Pearson's correlation: $P > 0.100$ in all cases), providing no evidence for density dependence in rates of parasitism.

Field manipulations

The proportion of aphids parasitised was not significantly affected by Edge or End distance (logistic regression: $P > 0.050$ in all cases); however floral (Patch) distance significantly affected rates of parasitism in all three trials (logistic regression: $P < 0.05$ in all cases). When data from all three trials were combined, the effect of proximity to floral resources was highly significant (logistic regression: $Z = 5.56$, $P < 0.001$) (Fig. 4.7).

Rates of parasitism were considerably lower inside the buckwheat patch (i.e., at 0 m) than at its edge (2 m), where they were at their highest (Fig. 4.7). Rates of parasitism then showed a negative exponential decline with increasing distance from the floral resource patches, such that proportion parasitised would be expected to reach less than 0.01 by 22 m and by 40m, mean rates of parasitism would be expected to be one-thousandth of those recorded at 2 m. In this experiment no parasitism events were recorded more than 14 m from the floral patches.

Table 4.1: Results of linear regressions on numbers of aphids and mummies (parasitised aphids) vs. distance from end of field (End), distance from nearest edge (Edge), and distance from nearest floral patch (Patch) in field surveys. * = P < 0.05, ** = P < 0.001 ____ = no aphids recorded.

		Aphids			Mummies		
Field	Survey	End	Edge	Patch	End	Edge	Patch
1	1	$F_{(1,54)} = 4.38$ * $R^2 = 0.075$	n.s.	n.s.	n.s.	n.s.	n.s.
1	2	n.s.	n.s.	n.s.	n.s.	$F_{(1,106)} = 10.87$** $R^2 = 0.093$	n.s.
2	3	n.s.	$F_{(1,49)} = 4.18$ * $R^2 = 0.079$	n.s.	n.s.	n.s.	n.s.
2	4	$F_{(1,59)} = 13.30$ ** $R^2 = 0.184$	n.s.	$F_{(1,59)} = 5.30$* $R^2 = 0.082$	n.s.	n.s.	n.s.
2	5	$F_{(1,67)} = 3.97$** $R^2 = 0.056$	$F_{(1,67)} = 8.27$** $R^2 = 0.110$	n.s.	n.s.	n.s.	n.s.
2	6	____	____	____	n.s.	n.s.	n.s.

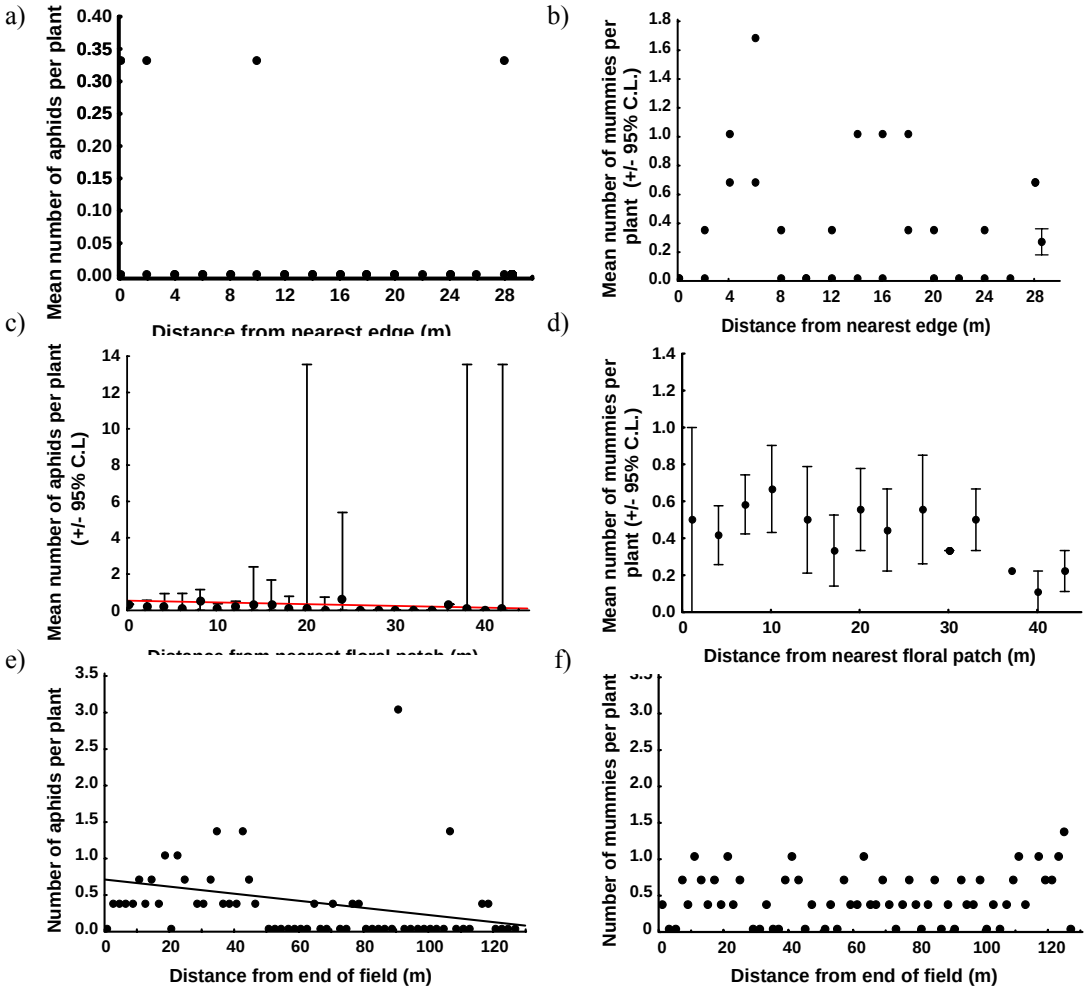


Figure 4.6: Regressions of distance from a) nearest edge, c) nearest floral patch and e) end of field on densities of *Metopolophium dirhodum*, and effects of the same variables on densities of *Aphidius* mummies (b), d) and f)). All results were obtained from Field 2 in surveys 2 (c), d), e) and f)) and 3 (a) and b)). Means and C.L. for c) are back-transformed from square-root transformed variables.

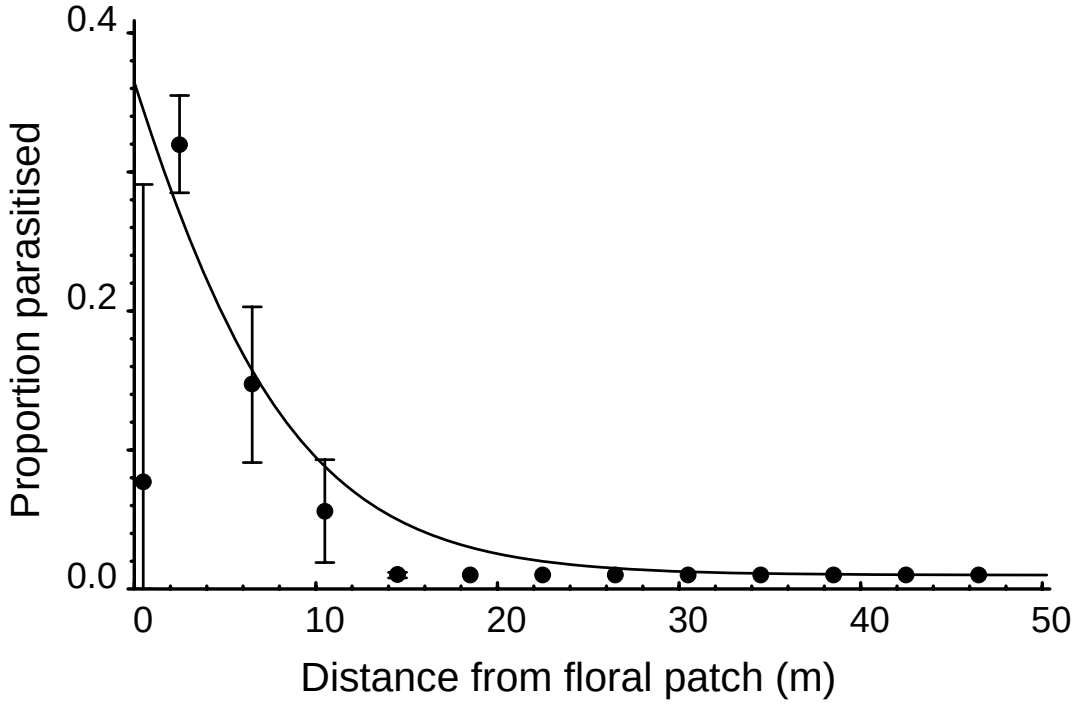


Figure 4.7: Mean (+/- 95% C.L.) proportion of experimentally placed *Metopolophium dirhodum* parasitised by *Aphidius rhopalosiphi* at increasing distances from the nearest floral resource patch. Means and C.L. are back-transformed from arcsine square-root transformed data. The equation of the line is y = exp (-.688 -.178x)/ (1+exp (-.688 - 178x)).

DISCUSSION

Laboratory and field experiments conclusively demonstrated that fitness advantages to parasitoids receiving floral resource subsidies translate into significant increases in rates of aphid parasitism. A combination of increased longevity and potential fecundity (egg load) resulted in a two-fold increase in realised fecundity for sugar feeding *Aphidius rhopalosiphi* in the laboratory. Flowering buckwheat plants caused a slight increase in rates of parasitism but this result was not statistically significant, presumably due to limitations on sample sizes (n = 4). Importantly, however, rates of parasitism in the buckwheat treatment were in the direction expected from laboratory studies (Chapter 3) and the data were in broad agreement with experiments testing the impact of buckwheat plants on *A. rhopalosiphi* parasitism under field conditions.

The strongest evidence for enhancement of parasitoids was obtained from the field manipulations. Rates of parasitism were greatly enhanced near floral patches, but decreased exponentially at increasing distances away from the patch. An effect was only obtained up to a maximum distance of 14 m, although weaker effects are predicted to persist at greater distances. Previous studies (e.g., Cameron & Walker 1989, Muratori *et al.* 2000, Brewer *et al.* 2001) have examined aphidiid population dispersal on a landscape scale, which is relevant to classical importation biological control. The present study, however, demonstrates the limited range of dispersal from floral resources on a smaller spatial scale germane to conservation biological control. For the biological control practitioner, the absence of parasitism at distances greater than 14 m from floral patches in the present study implies that strips of buckwheat would need to be planted a maximum of 28 m apart for observable resource subsidy effects to permeate the entire crop.

A similar result was obtained by Chaney (1998), using 1 m x 7 m strips of sweet alyssum *Lobularia maritime* (L.) (Brassicaceae) to enhance natural enemies of aphids (especially *Myzus persicae* [Sulzer]) on lettuces. Beneficial insect population densities increased near the floral resource, and aphid populations were reduced. The distance over which this effect was observed was in the order of 11m, as in the present study. Several other studies have shown similar effects on natural enemy densities (van Emden, 1962; Smith, 1969; Horn, 1981; Bugg *et al.*, 1991; Costello & Altieri, 1995; Theunissen *et al.*, 1995; Hickman & Wratten, 1996; Montandon & Slosser, 1996; Lehmhus *et al.*, 1996, 1999; Goller *et al.*, 1997; Vidal, 1997; Stephens *et al.* 1998), however, Berndt *et al.* (2002) found no effect of buckwheat resource subsidies on densities of female leafroller parasitoids, perhaps due to the high-density host patches produced by the release/recovery method. Rates of parasitism in the latter study were also unaffected by proximity to floral resources, but were high in all treatments, indicating that hosts, rather than floral resources were limiting this population (Berndt *et al.* 2002).

Incongruously, rates of parasitism were markedly lower on aphids within the buckwheat patches themselves than on the edges of the patches (Fig. 4.8). At face value this seems somewhat counter-intuitive, as parasitoids within the floral patches should have greatest access to resource subsidies, and should therefore be capable of exerting very high

levels of parasitism on aphids within the patch. However, this was clearly not the case for these data. Instead, the results are compatible with the concept of spatio-temporal partitioning between feeding and host-searching behaviours. Female parasitoids may respond to different visual or chemical cues at different times depending on their physiological state. For example, female parasitoids (Hymenoptera: Braconidae and Ichneumonidae) prefer food odours to host plant odours when starved of sugar supplements (Wäckers 1994, Jacob & Evans 2001). If the same holds true for female *A. rhopalosiphi* within buckwheat patches, then the data indicate that they may have been feeding rather than host-searching. Although empirical studies are limited, this phenomenon may be widespread and general among insect predators. For example, Hickman *et al*. (2001) found that gravid female hoverflies (Diptera: Syrphidae) were largely caught in traps closer to ground level, where prey were more abundant. Females caught in traps positioned at a height of 1 m were more likely to be immature females looking for floral resources with which to mature their eggs.

After feeding, female parasitoids are presumably stimulated primarily by host or host-plant odours, and move away from the floral patch. By chance alone, females are more likely to find proximally located host patches first, because as search radius increases the number of experimentally placed host patches per unit area decreases exponentially.

There was an interesting incongruence between the results of the field surveys and those of the experimental field manipulations. Whereas the clip-cage experiments showed high rates of parasitism close to floral resource patches, no such effect was observed in the surveys of natural populations. None of the environmental variables measured (i.e., 'Edge', leeward 'End' or floral 'Patch' distances) adequately explained levels of parasitism at natural aphid densities. There are several potential explanations for this disparity. First, aphid densities were constant in the manipulations, but varied in the surveys. If rates of parasitism per plant were primarily density dependent (e.g., Jarosik & Lapchin 2001), the manipulative experiments would highlight other determinants of parasitism (e.g., proximity to floral resources) that may otherwise be overwhelmed by effects of aphid density. However, no evidence for density dependence was found in this study. Levels of parasitism were not correlated with aphid density, either at the time mummies were observed, or

during the previous survey (the approximate time that parasitism would have occurred, allowing a seven day time-lag for mummification). It is possible that the spatial scale at which aphid density is important is finer than that of the surveys (i.e., within one plant or leaf, rather than a group of plants) (Jarosik & Lapchin 2001). Nevertheless, in surveys where aphid density was correlated with distance from the end of the field (probably due to a windbreak effect, e.g., Corbett & Rosenheim 1996) there was no concomitant effect on levels of parasitism.

An alternative explanation for the discrepancy between surveys and manipulative experiments relates to parasitoid population density. Abundance of parasitoids (measured by mean number of mummies per leaf) showed a marked decline from mid December onwards. This may have been due to a decline in aphid populations, or both species may have been affected by environmental factors. While parasitoid populations were at their peak during field surveys, however, competition may have been high among parasitoids. In this situation, a state-dependent ideal free distribution (SDIFD) model predicts that parasitoids would not leave the host patch to feed (Sirot & Bernstein 1996), resulting in no observable effects of floral resources on rates of parasitism. After the decline in parasitoid population levels, (intra- and perhaps interspecific) competition for food resources would also decline, making feeding an optimal strategy. It is at these times of low competition that the benefits of floral resources to biological control may be at their maximum.

It is also possible that while aphid and parasitoid population levels were high, hyperparasitoids and generalist predators may also have been more abundant. If these tertiary consumers are enhanced by floral resource subsidies in a manner analogous to *A. rhopalosiphi*, it may become disadvantageous for primary parasitoids to use floral resources at that time. Moreover, if mortality rates are high (e.g., due to high predation pressure), longevity of even well-fed individuals will be reduced. An SDIFD model predicts that in such circumstances instantaneous reproductive success should be maximised and individuals should chose to host-search/oviposit rather than feed (Sirot & Bernstein 1996). As populations of aphids and parasitoids declined, high populations of hyperparasitoids and generalist predators could no longer be sustained, and there may have been a shift in optimal parasitoid strategy, toward increased utilisation of floral resources.

High competition and mortality risks may therefore reduce the effectiveness of floral resource patches as a tool for biological control. However, these conditions will only operate at certain times, and the effectiveness of floral subsidies in the remainder of the season was significant.

In conclusion, resource subsidies enhance both potential and realised fecundity of *A. rhopalosiphi*, in both artificial and natural conditions. However, other factors may affect natural rates of parasitism to the extent that enhancement by floral resources is difficult to detect at certain spatial or temporal scales. If buckwheat is to be used to commercially enhance *A. rhopalosiphi*, resource patches should be located no more than 28 m apart, although the patch size required for enhancement remains to be determined. Moreover, use of any floral resource subsidies is dependent upon information being available on economic damage thresholds for the pest species under study (Watt & Wratten 1984; Mann & Wratten 1991) and flowering plant species attributes, for example, phenology of flowering (Bowie *et al.* 1995) and quality of nectar resources (Davis *et al.* 1998; Wäckers 2001).

CHAPTER 5: OVERALL DISCUSSION AND CONCLUSIONS

Summary of results

Ecological theory has much to offer biological control. Informed use of resource subsidies for different life-history stages of natural enemies allows them to better reduce populations of their hosts or prey. The present study demonstrates that floral resource subsidies enhance rates of aphid parasitism by *Aphidius rhopalosiphi*, and that the mechanisms resulting in this enhancement may operate generally among the Aphidiidae.

Longevity and potential fecundity of *A. rhopalosiphi* and *Diaeretiella rapae* were significantly enhanced by sugar-based resource subsidies. Moreover, realised fecundity of *A. rhopalosiphi* (measured by rates of parasitism in the laboratory) increased significantly when sugar was provided. Such patterns of enhancement of parasitism rates are consistent with other studies of aphidiid (Arthur 1944, Starý 1964; Singh *et al.* 2000b) and non-aphidiid (Dyer & Landis 1996; Jacob & Evans 2000; Sagarra *et* al. 2001; Irvin *et al.* in press) parasitoids, and provide mechanistic explanations for the enhancement of the efficacy of natural populations of parasitoids in the presence of floral resources (e.g., Chaney 1998).

Naturally occurring rates of parasitism in an unmanipulated field environment were not significantly affected by floral resources in the present study. This may have been the result of stochasticity of aphid densities masking the effects of resource subsidies, although rates of parasitism were not directly correlated with aphid density at the spatial scale measured. When aphid density was experimentally manipulated, however, significant

effects of the proximity to floral resources on rates of parasitism were revealed. The proportion of experimentally-placed aphids that were parasitised decreased exponentially as the distance from floral resource patches increased. No parasitism was recorded at distances greater than 14 m from the nearest floral patch. Beneficial effects of floral resources (sweet alyssum *Lobularia maritima* (L.) Brassicaceae) on aphid natural enemy densities have been reported previously at a similar scale of distance (Chaney 1998).

The benefits of floral feeding for the parasitoid will depend on the quantity and temporal availability of resources consumed (Siekmann *et al.* 2001), which in turn depend on the time spent feeding. If subsidies are obtained from hosts, for example, by host feeding or from aphid honeydew resources, food and host searching may take place at the same time, governed by the same chemical cues (Budenberg 1990; Longley & Jepson 1996; Du *et al*. 1997; Shaltiel & Ayal 1998). However, if food patches are spatially and/or temporally separated from host patches, different factors may determine the trade-off in time spent feeding versus host-searching. For example, physiological thresholds relating to age, egg load and nutritional status, resource availability and mortality risk may determine the optimal time spent feeding or host-searching (Wäckers 1994; Sirot & Bernstein 1996; Rivero & Casas 1999a). Costs associated with increased mortality risk or time-limited sub-optimal exploitation of host patches, may limit the amount of time spent foraging for food (Sirot & Bernstein 1996). In order to maximise reproductive success, these costs must be outweighed by the fitness advantages of feeding on floral resources.

Costs associated with floral feeding

There are direct and indirect costs associated with floral feeding for parasitoids. Direct predation may lead to higher mortality of parasitoids at close proximity to floral patches. If densities of aphidiid natural enemies are highest at close proximity to floral resources, and rates of predation and hyperparasitism show an exponential decay similar to rates of parasitism by *A. rhopalosiphi*, then adults feeding on flowers will be more likely to be preyed upon, and larvae (which were at high density close to floral resources) will be more likely to suffer secondary parasitism. The presence of predators or hyperparasitoids may therefore reduce survival of aphidiid adults (reviewed in Rosenheim 1998) and larvae (Burton & Starks 1977, Ferguson & Stiling 1996), or alternatively, modify their behaviour such that individuals more readily leave patches containing higher-order predators (Höller *et al*. 1993; Petersen *et al.* 2000; but see Völkl *et al.* 1995; Raymond *et al.* 2000). Predator-mediated departure from host patches may reduce aphid natural enemy efficacy (Burton & Starks 1977; Höller *et al*. 1993; Mackauer & Völkl 1993; Rosenheim 1998), and high adult mortality rates (for any reason, including predation), cause individuals to leave floral patches after intermediate levels of feeding rather than achieving complete satiation (Sirot & Bernstein 1996).

It is reasonable to assume that while natural enemies of aphids are attracted by floral resources and benefit from resource subsidies, so too may be natural enemies of the parasitoids themselves. Although the vast majority of studies focus on enhancement of primary parasitoids by floral feeding, hyperparasitoids of aphidiids have also been observed to visit flowers (Jervis *et al*. 1993). Although the effects of floral feeding on

hyperparasitoid efficacy remain to be determined, a primary parasitoid (*Anacharis* sp.) has been shown to benefit from floral buckwheat resources resulting in lower population densities of a beneficial lacewing (*Micromus tasmaniae* Walker) (Stephens *et al*. 1998). Such enhancement of higher-trophic level parasitoids or predators by floral resource subsidies is potentially inimical to conservation biological control outcomes. However, if it is possible to select plants or sugars that are able to be utilised by natural enemies and not pests (Baggen & Gurr 1998; Wäckers 2001), it may be possible to similarly select plants with resources that natural enemies can utilise, but that are unavailable to pests or to higher order predators.

Indirect costs associated with floral feeding are that individuals who choose to feed temporarily on flowers forego the opportunity to search for hosts or mates (Sirot & Bernstein 1996; Lewis *et al.* 1998; Jacob & Evans 2001). This may be of particular importance in situations where competition for hosts is great, or floral resources are widely separated from host patches, incurring greater costs in terms of travelling time and energy expenditure. A number of studies of host-feeding parasitoids have examined the opportunity costs associated with feeding rather than ovipositing on hosts (e.g., Heimpel & Rosenheim 1995; Rivero & Casas 1999). It was found that high host availability, long life-expectancy and high egg loads favoured investment in future reproduction (i.e., host feeding) over current reproduction (i.e., oviposition) (Heimpel & Rosenheim 1995). Although *Aphidius* does not host feed, the time costs associated with floral feeding still require a 'decision' whether to maximise current reproduction (via host-searching and oviposition) over future reproductive potential (via floral feeding).

When will resource subsidies be useful?

In order for floral resource subsidies to increase parasitoid efficacy, as has been demonstrated in the present study, the potential costs associated with floral feeding must be outweighed by the benefits of increased fecundity. It is not imperative that the fitness benefits of increases in longevity and fecundity occur simultaneously. Rather, they may manifest themselves to varying degrees at different times. For example, increases in longevity will be most beneficial in time-limited populations of natural enemies, where host densities are low (Rosenheim 1996). Increased longevity provides parasitoids with more time for host-searching, allowing an increase in the total number of hosts located and, consequently, increased lifetime reproductive success. Additionally, if a parasitoid species has evolved a strategy of producing numerous relatively small eggs, at little cost per egg, the probability of becoming time limited increases, as more hosts are required for the additional eggs. In terms of the model used by Rosenheim (1996), as egg size *s* decreases, the time at which egg supply is exhausted, before which parasitoid death constitutes time limitation, is extended. This time (*R/sk* days, where *R* equals the resources available for reproduction and *k* is the daily host encounter rate) increases further if resource subsidies allow an increase in the physiological resources allocated to reproduction (*R*), as the present study demonstrates.

Increased longevity also increases the likelihood of finding a mate when parasitoid population densities are low. Similarly, increased longevity improves statistically the chances of finding a mate of higher quality, which is related to body size in aphidiid (Cloutier *et al.* 2000) and non-aphidiid (Petersen & Hardy 1996; Boivin & Lagace 1999; Lauziere *et al*. 2000; Sagarra *et al*. 2001) parasitoids. Either of these scenarios potentially

leads to improved offspring fitness (Michaud 1994; Eberhard 1996; Birkhead & Møller 1998).

It is important to note, however, that there are circumstances under which increased longevity may have little impact on lifetime reproductive success. For example, if longevity were generally determined by extrinsic factors such as predation, rather than intrinsic physiological constraints, then resource subsidies would be relatively unimportant.

Additionally, if a population is predominantly egg limited, individuals are, by definition, exhausting their maximum egg supply before death, so that extending this post-exhaustion period would provide no additional fitness benefits. Even if additional eggs are matured throughout the female's lifetime, maturation rate can decline with age (Rosenheim *et al.* 2000). Moreover, female parasitoids show a tendency to produce a higher proportion of male offspring later in life (despite multiple mating episodes) (reviewed in Starý 1970), which may represent sub-optimal fitness rewards in terms of reproductive success of the F_1 generation. A preference for female offspring is evident in the predominant female-bias of aphidiid populations (Starý 1970), and the greater number of haploid (male) eggs laid by *Lysiphlebus delhiensis* (Subba-Rao & Sharma) (Hymenoptera: Aphidiidae) in unsuitable host stages (Srivastava & Singh 1995). The above mechanisms may serve to reduce with age the fitness benefit to parasitoids experiencing increased longevity.

Situations in which parasitoids are predicted to gain maximum advantages from increased longevity (e.g., where predation rates are low, mate encounter rates are low, or hosts are rare), tend to occur at the beginning and end of the crop season. In the present study, population densities of *A. rhopalosiphi* and *M. dirhodum* were at their lowest at the beginning and end of the summer, and presumably could not sustain high densities of

fourth trophic level predators. These conditions would lead to time-limitation of the *A. rhopalosiphi* population. Conversely, in mid-summer (December), aphid population densities are often at their highest (Wratten & Powell 1990) and parasitoids are more likely to be egg limited. Parasitoid densities are also high at this time, and could potentially sustain high population densities of predators and hyperparasitoids. At this time, fitness benefits from enhanced longevity would be minimal, however, benefits of increased egg load would be at their maximum. Egg load increases are of no value when the numbers of hosts limit reproductive success. However, if hosts are abundant, as they are mid-season, egg limitation is more likely to occur and resource subsidy-based enhancement of fecundity is of paramount importance. As intraspecific competition is at its peak mid-season (due to high parasitoid densities), a state-dependent ideal free distribution model predicts that leaving the host patch to search for food is not the optimal strategy at this time (Sirot & Bernstein 1996). However, leaving the host patch may be unnecessary, as high aphid densities would produce large quantities of honeydew. Floral resources may therefore be most important at times when aphid densities are low, and other non-floral resources (e.g., aphid honeydew) are unavailable. Knowledge of early-season agronomy and phenology of flowers is therefore crucial if floral resources are to be available at the times at which they are most beneficial (Bowie *et al*. 1995).

Conclusions

The ecologically depauperate nature of conventional agricultural ecosystems is highlighted by the fact that a simple addition of flowering plants can increase biological control of crop pests by natural enemies. There is no support for the classical assumption

that high population densities of biological control agents capable of exerting top-down control can be sustained by the resources present in a crop system alone. Food-web ecology has challenged and rejected the discrete trophic level paradigm in favour of complex multispecies interaction-webs, characterised by multichannel omnivory and indirect interactions (e.g., Hawkins 1992; Polis 1994; Polis & Strong 1996). It is the many weak interactions with non-host species and the environment that have largely been overlooked in classical biological control. Understanding these interactions not only reduces the probability of unforeseen environmental harm through control agents becoming invasive (e.g., Strong & Pemberton 2001), but also provides the theoretical tools necessary for successful biological control (Lewis *et al.* 1998, Berryman 1999; Gurr & Wratten 1999; Gurr & Wratten 2000b; Landis *et al.* 2000). Identification and provision of resource subsidies to natural enemies allows the practical application of ecological theory to biological control in natural and modified landscapes.

The present study demonstrates the potential utility of buckwheat for enhancement of aphid parasitoid efficacy. However, the spatial scale over which beneficial effects were observed was relatively small, and planting buckwheat strips every 28 m within a wheat field may not be commercially viable. However, a different plant species may produce a stronger effect, or one that does not decrease as rapidly across space. Laboratory experiments can be used to compare a range of candidate plant species for the enhancement of natural enemy efficacy (e.g., Patt *et* al. 1997a).

The enhancement of *A. rhopalosiphi* by floral resources therefore supports the concept of habitat management for biological control, but the small spatial scale of enhancement implies that other methods of control may be required to combine with floral

resource patches, so as to form an effective IPM system (Gurr & Wratten 1999; Landis *et al*. 2000).

In ecological terms, the present study has shown that bottom-up (with respect to the parasitoid, rather than the herbivore) floral resource subsidies allow parasitoids to maximise their reproductive success via increases in longevity and egg load, thereby improving top-down (recipient) control of aphid pests. This seemingly paradoxical statement illustrates the point that even systems that appear to be structured by recipient control may often be partially or wholly donor (bottom-up) controlled (Hawkins 1992; Polis & Strong 1996; Rosenheim 1998; Williams *et al.* 2001). Therefore, food-web engineering by provision of floral resource subsidies is not effective only in the practical enhancement of a specific biological control agent, but its use is based on a sound foundation in ecological theory that allows extension of these principles across taxa. Combining theoretical and practical approaches to biological control is imperative if success rates are to improve such that agricultural independence from pesticides may become sustainable.

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